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**Projected Sea Level Rise and the Conservation Ecology of
the Micronesian Megapode (*Megapodius laperouse senex*) in
Palau, Micronesia**

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ABSTRACT

Climate change has been a subject of numerous studies. While findings suggest that most biological taxa will be affected by its manifestations, aspects of a species life history may increase its susceptibility to climate change. Given their reliance on environmental sources of heat to incubate their eggs, I examined the vulnerability to climate change of the avian family Megapodiidae. I also assessed habitat use, susceptibility to sea level rise, and the effect of introduced rats and tourist presence, as added stressors to climate change, on the Micronesian Megapode (*Megapodius laperouse senex*) in Palau.

Based on available literature, I employed a trait-based assessment to investigate the vulnerability of 21 species of megapodes to climate change. All species were predicted to experience at least a 2°C increase in mean annual temperature, 12 may experience a moderate or greater fluctuation in rainfall, and 16 would be exposed to rising seas. While the most vulnerable megapodes are intrinsically rare and range restricted, mound nesting species may be more resilient to climate change than others.

I examined breeding and foraging habitat use by the mound nesting megapode in the Rock Islands Southern Lagoon Conservation Area (RISL), where it almost exclusively uses low-lying littoral strand habitat for breeding. Megapodes preferentially selected sites that were 1) relatively close to shore, 2) contained large trees, and 3) exhibited greater canopy heights than the surrounding forest. The subspecies foraged in a non-preferential manner and used all littoral habitat with no apparent influence of dominant plant species composition.

Using GIS and the latest spatial data, I modelled the effect of three currently accepted scenarios (0.52 m, 0.98 m, and 1.9 m) of sea level rise on their known breeding habitat. The RISL is comprised of 3,857.5 ha of forested cover of which megapodes used 120.8 ha (3.1%) for breeding, with an additional 25.3 ha potentially available to them. Megapodes may lose at least 32.5% to 43.3% of known breeding habitat and 25.7% to 31.3% of potential habitat to inundation, respectively.

Using passive chew-tag and call playback surveys, I examined whether introduced rats and tourist presence may negatively affect megapodes in the RISL. Rat detection probability and site occupancy were significantly higher on tourist visited

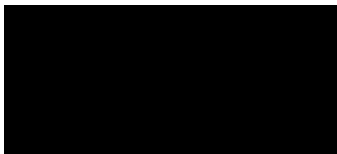
(89% and 99%, respectively) compared to tourist-free islands (52% and 73%). I detected significantly more megapodes at stations on tourist-free islands (93%) than tourist visited (47%), but relative abundance was not significantly different between island types. My findings suggested no significant relationship between rats and megapodes, a negative relationship between tourist presence and megapodes, and augmentation of rat populations by tourist presence.

I compared the ecology of, and IUCN listed threats for, Micronesian Megapodes in Palau with those in the Mariana Islands. I proposed both the inclusion of an additional climate change related threat based on my sea level rise modelling, and new ranking of all IUCN threats by subspecies. Lastly, I proposed research and data acquisition priorities necessary to fill current gaps in the knowledge of megapodes in Palau and facilitate its long-term conservation.

DECLARATION

I certify that this thesis does not, to the best of my knowledge and belief:

- i. incorporate without acknowledgement any material previously submitted for a degree or diploma at any institution of higher education;
- ii. contain any material previously published or written by another person, except where due reference is made in the text of this thesis; or
- iii. contain any defamatory material.



Paul Radley

12 January 2019

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- World Pheasant Association: *Projected Sea Level Rise and the Conservation Ecology of the Micronesian Megapode* (Megapodius laperouse senex) in Palau, Micronesia

PUBLICATIONS ARISING FROM THIS RESEARCH

I have compiled this thesis in the format of ‘thesis with publication’. Chapters 2 is presented as a reformatted copy of the published article, and Chapter 5 as the manuscript I have submitted for review. Some repetition of site description and methodology is therefore unavoidable throughout this thesis. I have not reproduced the original abstract of the paper resulting from Chapter 2, but I have included the relevant acknowledgements sections for each paper and have incorporated the references for each into the single list that serves the entire thesis. I warrant that, where necessary, I have obtained permission to use in this thesis any of my own published work for which the copyright is held by another party.

Chapter 2

Radley, P.M., R.A. Davis, R.W.R.J. Dekker, S.W. Molloy, D. Blake, and R. Heinsohn. 2018. Vulnerability of megapodes (Megapodiidae, Aves) to climate change and related threats. *Environmental Conservation*: DOI 10.1017/S0376892918000152

Chapter 4

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CHAPTER 1: General Introduction and Study Site Description

Climate change has been the topic of numerous studies over the past few decades, scrutiny that is warranted given its predicted impacts to global biodiversity (e.g., Thomas *et al.* 2004; Araujo & Rahbek 2006; Lovejoy 2008; Dawson *et al.* 2011; Bellard *et al.* 2012). Findings strongly suggest that every ecosystem and landmass will be affected by climate change and all of its associated environmental manifestations (Collins *et al.* 2013). Most biological taxa will likewise be affected, some responding to changes in local climate through shifts or increases in their geographic ranges (Thomas *et al.* 2004; Thuiller 2007; Thomas 2010). Populations of others will be forced into decreased or contracted ranges (particularly on mountains and towards the poles), while others still may experience a drastic if not complete loss of habitable area, ultimately leading to local extinction of those not able to adapt or shift their niches as needed (Colwell *et al.* 2008; Chen *et al.* 2011; Engler *et al.* 2011; Bellard *et al.* 2012; Wiens 2016).

Globally, Foden *et al.* (2008) predicted that approximately 35% of the world's avifauna is highly susceptible to climate change. Those species most at threat are endemic to the tropics, many confined to relatively small and restricted ranges (Jetz *et al.* 2007; Lovejoy 2008; Sekercioglu *et al.* 2012). The majority of these threatened species tend to be sedentary, endemic to mountain tops or lowland areas (with no access to higher, temperate elevations), and coastal forest birds or other range-restricted species such as those occurring on islands (Sekercioglu *et al.* 2012). While species on larger landmasses in more temperate latitudes may have avenues available to escape the near term effects of a changing climate (McCarty 2001; Thomas 2010), those on small and relatively isolated tropical islands may not (Kingsford & Watson 2011; Taylor & Kumar 2016). Terrestrial species of these insular oceanic ecosystems will be threatened by both increasing temperatures and fluctuations in rainfall (Corlett 2014). Unlike the primary threats to taxa of continents and larger islands, however, terrestrial species of Pacific islands may be most threatened by the seas that surround them (Church *et al.* 2006; Nunn *et al.* 2015; Taylor 2017).

The current epoch of eustatic or global sea level rise is not a contemporary phenomenon but one that has been recorded occurring for more than the past century

(Church *et al.* 2013). For the 1 million years prior to this, eustatic high stands were relatively routine events and coincided with the waning of ice ages and the resulting interglacial maxima (Ramstein 2011). Numerous terrestrial taxa of Oceania are predicted to be threatened by current projections for future sea level rise, with endemic birds topping the list given their tendency to occur on small, isolated islands (Wetzel *et al.* 2013). Amongst the particularly threatened bird species may be those that belong to the avian family Megapodiidae.

Megapodes and Climate Change

Some life history and ecological traits of megapodes may render them particularly susceptible to the manifestations of climate change. The family comprises 22 species distributed throughout the central Indo-Pacific and Australasia (Jones *et al.* 1995; Harris *et al.* 2014). Ranging broadly west to east from the Nicobar Islands in the Indian Ocean to Tonga in the Pacific, and north to south from Uracus in the Mariana archipelago to very southern portions of Australia, megapodes occur everywhere from small oceanic islands to large continent-sized landmasses (Jones *et al.* 1995). All but two species are confined to the tropics and at least 16 range below 2000 meters in elevation (Jones *et al.* 1995; IUCN 2016). Most megapodes rely on moist lowland to montane forests, while a smaller contingent occur in cover types ranging from dry forest to coastal forests in supratidal areas (Jones *et al.* 1995; IUCN 2016).

Megapodes are strictly ground nesters that do not use body heat to incubate their eggs. Instead, they employ three biological or environmental sources of heat; 1) microbial decomposition of organic matter, 2) volcanic or geothermal activity, and 3) passive solar radiation (Jones *et al.* 1995; Sinclair 2002). Unlike any other birds, megapodes rely directly and exclusively on elements of their immediate, external environment for a critical component of their reproduction. Specifically, 18 species use microbial decomposition for incubation (12 rely on this method exclusively) and require organic biomass collected from the forested habitat in which they establish their incubation sites (Jones *et al.* 1995). Such incubation sites consist of either a mound of soil or a burrow, both of which are filled with leaves and fine woody debris (Jones *et al.* 1995; Sinclair 2002). These same species predominantly require relatively cool, humid, stable forest microclimates to maintain efficient incubation. Optimal incubation

temperatures for most megapodes is 35° C, with hatching success drastically reduced when mound or borrow temperatures fall below 32° C and rise above 38° C (Jones *et al.* 1995). Much of the cumulative range of the megapodes is predicted to experience future increases in temperature and decreased or more seasonal rainfall (Collins *et al.* 2013). Combined with human forestry practices throughout parts of their range (Cochrane 2003; Brodie *et al.* 2012; Diffenbaugh & Giorgi 2012), these changing conditions could be exceedingly detrimental to the availability of both biomass and areas of suitable microclimate necessary for incubation by most species of megapodes.

Given their ground nesting habits, megapodes may be more affected by inundation by sea level rise than most other landbirds. Twelve species incubate their eggs to some extent within relative close proximity to the ocean and high tide (Jones *et al.* 1995), six of which occur in biodiversity hotspots predicted by Bellard *et al.* (2014b) to be highly impacted by sea level rise. Populations of the Nicobar Megapode (*Megapodius nicobariensis*), Moluccan Megapode (*Eulipoa wallacei*) and the Palau subspecies of the Micronesian Megapode (*Megapodius laperouse senex*), place their incubation sites closer to shore than all others.

The Micronesian Megapode is the focus of my study detailed in this thesis, and Palau serves as the model system for examining the synergistic effect of sea level rise, introduced rats and tourist pressure on the ecology of the subspecies.

Sea Level Rise and the Micronesian Megapode

Owing to their high exposure to external climate and ocean processes, coastal areas of oceanic Pacific islands are particularly vulnerable to the manifestations of climate change including increased storm frequency and intensity, changes in wind, wave, and rainfall regimes, and inundation by rising seas (Nicholls & Cazenave 2010; Nunn *et al.* 2015). Species that concentrate their breeding activities along coastal areas of these islands may experience greater exposure to flooding and inundation, particularly when driven by storm waves at higher mean sea levels (Reynolds *et al.* 2015; Reynolds *et al.* 2017).

Unlike the Micronesian Megapode in the Mariana Islands (*M. l. laperouse*), those in Palau strictly employ microbial decomposition of organic matter to incubate

their eggs (USFWS 1998; Olsen *et al.* 2013; Olsen *et al.* 2016). Fifty-five percent of active megapode mounds in Palau occur in the UNESCO World Heritage listed Rock Islands Southern Lagoon Conservation Area (RISL) and 31% on Kayangel Atoll in the northern portion of the archipelago (Olsen *et al.* 2016). In both locations, megapodes most commonly build their mounds just above high tide in littoral strand forest of the sandy beach areas associated with many of the eroded karst islands in the lagoon (Olsen *et al.* 2016). Given the proximity of their mounds and the susceptibility of their breeding habitat to high tide, megapodes in Palau are particularly and highly threatened by sea level rise inundation.

Other birds of the Pacific are similarly threatened by rising seas (e.g., Reynolds *et al.* 2012; Wetzel *et al.* 2013; Reynolds *et al.* 2015). Work by other researchers (e.g., Cibois *et al.* 2010; Thibault & Cibois 2017) indicates that to survive past eustatic high stands of the Quaternary Period, currently extant species of insular landbirds managed to secure refuge from inundation on other nearby, higher islands. One possible strategy for survival for the megapode in Palau is locating and utilizing areas on their current or neighbouring islands that will be least affected by sea level rise. Such areas may consist of substrate and habitat suitable for breeding by the mound building subspecies that occur above the projected upper limits of inundation for the archipelago. Considering that the last eustatic high stand was ~ 125,000 years ago, when Pacific sea levels reached on average approximately 6 m above the present (Steadman 2006; Cibois *et al.* 2010) this subspecies may have successfully faced this challenge previously.

Added Stressors for Megapodes in Palau

Megapodes in Palau are confronted by the dual threats and pressures placed on them by introduced rats and heavy tourist presence in the RISL. Introduced predators have contributed to the extinction of more than 50% of the world's island birds, with rats (*Rattus* sp) perhaps the most destructive (Towns *et al.* 2006; Doherty *et al.* 2016). Established on nearly 90% of islands globally, rats are well documented as a severe and exceedingly detrimental threat to island avifauna (e.g., Courchamp *et al.* 2003; Towns *et al.* 2006; Shiels *et al.* 2013; Harper & Bunbury 2015; Spatz *et al.* 2017). For island species threatened by climate change, rats and other invasive species may serve as compound or added stressors that potentially act to magnify the impact of climate

change itself (Brook *et al.* 2008; King & Finch 2013). Sources suggest that introduced rats are a direct threat to Micronesian Megapodes in both the Mariana and Palau archipelagos, but none cite any direct, quantitative evidence to justify this assertion (USFWS 1998; Wiles & Conry 2001; Olsen *et al.* 2013). Four species of rat have become established in Palau, two of which—the Polynesian rat (*R. exulans*) and black rat (*R. rattus*)—occur in forested areas (Wiles & Conry 1990).

The effect of nature-based tourism and recreation on global bird populations has drawn relatively little attention in either public or academic forums (Steven *et al.* 2011; Steven & Castley 2013). Of the 35 recognized global biodiversity hotspots (Myers *et al.* 2000), Polynesia-Micronesia is not only amongst the top three most vulnerable to climate change, but it also supports the most bird species threatened by tourism (Steven & Castley 2013; Bellard *et al.* 2014b). Steven and Castley (2013) determined that 63 birds listed as Critically Endangered and Endangered by the IUCN (2016) are directly threatened by tourism, and that species occurring in coastal areas are amongst those most at risk. Vying with the Maldives, Palau is one of the world's top SCUBA diving destinations (IMF 2016), and the majority of this activity occurs in and around the RISL. Several islands in the conservation area provide large beach areas that are favoured as rest and meal sites by dive operators. These beaches are equipped with developed picnic areas that include permanent covered shelters, grills for food preparation, and restroom facilities. It is not unusual for many dozens of tourists to visit these littoral areas on a daily basis, spending a couple of hours eating and exploring the strand forest (pers. obs., P. Radley). Many of these beach and coastal areas are also preferred breeding sites for megapodes in the RISL, some of them supporting relatively high numbers of birds and active incubation mounds.

Study Location and Description

The Palau archipelago (7° 30' N, 134° 35' E; Figure 1.1) is the westernmost assemblage of islands in Micronesia and dates back more than 30 million years geologically to the late Oligocene (Neall & Trewick 2008). It extends 700 km northeast to southwest and is comprised of 12 inhabited islands and well over 500 smaller uninhabited islands and islets (Neall & Trewick 2008; Olsen 2009). The climate is marine tropical with a mean

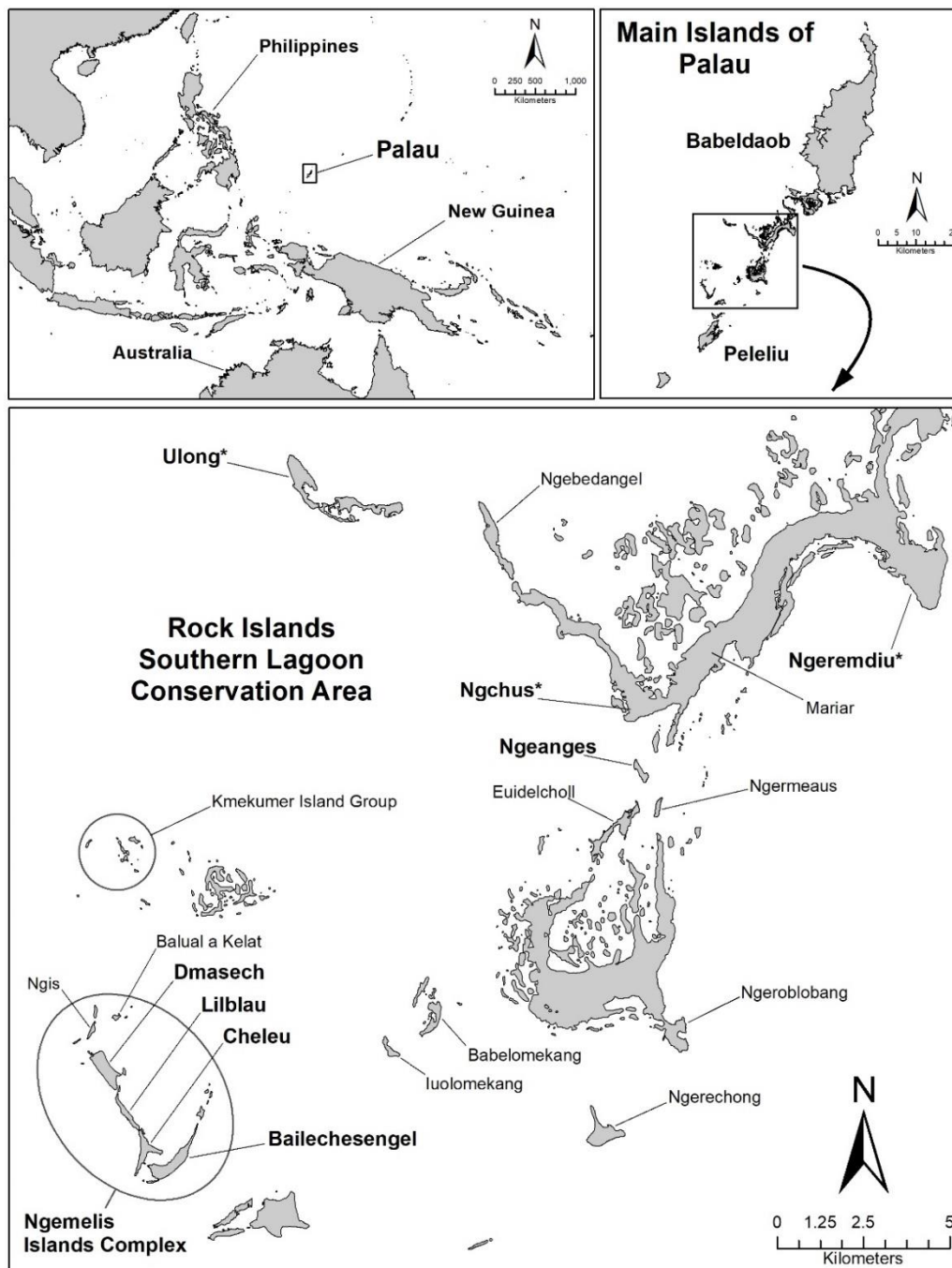


Figure 1. 1. Map of the study area including the geographic location of Palau and details of the Rock Islands Southern Lagoon Conservation Area. Mound locations were collected from all islands, island areas or groups labelled in the bottom panel. Individual islands labelled in bold font are those on which the majority of field activity occurred, those marked with an asterisk are tourist visited.

temperature of 27° C, a mean humidity of 82%, and an average annual rainfall of 380 cm, with July to October considered the wet season (Costion 2007). The flora of Palau

is predominantly broad-leaved evergreen moist forest (Costion 2007). Approximately 87 percent of the archipelago is forested, 75% of which is classified as native tropical lowland rainforest (Kitalong *et al.* 2013).

My research was focused primarily on the islands of the RISL, which lies between the island of Babeldaob to the north and Peleliu to the southwest (Figure 1.1). Megapodes are known to be more abundant here than anywhere else in Palau (Olsen *et al.* 2016). Unlike other islands in the archipelago, the “rock islands” in the RISL are ancient, uplifted reefs and thus coralline in nature (Engbring 1988). Although some have flat, sandy littoral zones that are moderately to heavily visited by tourists, most are uninhabitable by humans and characterized by sheer, highly fissured and eroded karst or limestone slopes that are typically undercut at the water’s edge, and covered by dense forest despite little or no soil development beneath (Pratt *et al.* 1980; Engbring 1988). Tourist-visited islands are additionally characterized by the presence of picnic and restroom facilities situated in cleared and maintained areas just off the beach.

Although mound location data for sea level rise modeling (Chapter 3) were collected on 19 islands or island areas or groups within the RISL, the majority of my research was carried out on 10 of them (Figure 1.1). For the purpose of my investigation of the effects of tourists and rats on megapodes (Chapter 4), five of these 10 islands were visited by tourists and five were tourist-free with only occasional human presence. Four of these latter islands were in a designated Koror State Government conservation area known as the Ngemelis Complex, where only locals had access without the need for a permit.

Study Rationale and Goals

Megapodes in general are likely to be highly threatened by climate change. The greatest potential threat to the Micronesian Megapode in Palau is projected future sea level rise, the effects of which to the subspecies may be exacerbated by both introduced rats and a heavy tourist presence. In this thesis, I use a literature review and published climate data to determine the potential effects of climate change on the megapodes as a whole. I follow this with field based studies to define the components of both breeding and foraging habitat that are important to the Micronesian Megapode in the RISL of Palau, and then assess the effect of sea level rise on both. I then evaluate the effect of

rats and nature-based tourism, and investigate the role they play as additional stressors to sea level rise for megapodes in the RISL. My thesis is structured around five primary objectives:

- Objective 1.* Quantitatively assess the threats of climate change to the megapodes based on their biological or ecological traits that may be most affected (Chapter 2).
- Objective 2.* Define the nesting and foraging habitat used by the Micronesian Megapode in the RISL of Palau (Chapter 3).
- Objective 3.* Investigate the effect of projected sea level rise on megapode foraging and breeding habitat in the RISL and identify possible refugia within the archipelago (Chapter 4).
- Objective 4.* Determine the effect that introduced rats and tourists have on megapodes in the RISL as added stressors to sea level rise (Chapter 5).
- Objective 5.* Examine the role that tourist presence plays in maintaining and augmenting rat populations in the RISL (Chapter 5).

The findings of my four primary chapters are integrated into a synthesis in a final chapter that explores the synergistic effect of climate change and external, added stressors as threats to an endangered species of island bird. One of the original intents of this study was to examine movement patterns of megapodes in the RISL via radio-telemetry and gene flow via molecular analysis. This would have provided a basis to infer how the subspecies may have dealt with the effect of previous eustatic high stands during the Pleistocene, and to predict how it may respond to the future scenarios it may be confronted with. However, a lack of success catching birds, and a lack of field time and autonomy resulting from my dependence on the Koror State Government for boat transportation (as discussed in Appendix A), in part lead to these objectives being excised from my study. Conversations with a team studying Micronesian Megapodes in the Northern Mariana Islands shed light on the difficulties of safely attaching transmitters to the species and further prompted me to reject the use of the method for birds in Palau.

CHAPTER 2: Vulnerability of Megapodes (Megapodiidae, Aves) to Climate Change and Related Threats

This chapter is not included in this version of the thesis.

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CHAPTER 3: Breeding and Foraging Habitat Ecology of the Micronesian Megapode in Palau

Introduction

In Chapter 2, I investigated how the predicted manifestations of climate change may affect the world's megapodes. All species will be impacted by climate change to at least some degree, while those most affected are rare species that are confined to relatively small and restricted ranges, such as islands. As a family of bird that depends exclusively on elements of its environment for reproduction, knowledge of habitat use by the Micronesian Megapode (*Megapodius laperouse senex*) in Palau is necessary to understand the effect that climate change may have on the subspecies.

Knowledge of a species' use of habitat is essential to understand its ecology and to address many of the environmental challenges it may face (Kays *et al.* 2011). Numerous species of temperate and tropical island birds are confronted not only with current threats presented by introduced predators and habitat loss, but also by future threats posed by climate change (e.g., Blackburn *et al.* 2004; Kingsford & Watson 2011; Sekercioglu *et al.* 2012; Taylor & Kumar 2016). Although the effects of climate change on avian species of the world's temperate areas are relatively well studied and understood, far more research on birds of the tropics is necessary (Sekercioglu *et al.* 2012). To formulate effective conservation action to counter the impacts of climate change on tropical birds it is essential to acquire more basic ecological information for them, including detailed data pertaining to their habitat requirements, which are lacking for many (Sekercioglu *et al.* 2012).

Climate change driven sea level rise will affect and drastically alter coastal habitats globally (IPCC 2007), which will in turn affect myriad populations of avian species that rely on them as sites for roosting, foraging and breeding (Clausen & Clausen 2014). Numerous species of waterfowl, shorebirds and seabirds are increasingly threatened as their breeding habitat is predicted to be inundated or washed away by rising seas or storm surges (e.g., Seavey *et al.* 2011; Craik *et al.* 2015; Ivajnsiĉ *et al.* 2017), the frequency and magnitude of which are expected to increase as a result of climate change (Collins *et al.* 2013). Some passerines, and shorebirds in particular,

are under further pressure as foraging habitat they rely on at migration stopover sites is likewise predicted to be inundated (e.g., Galbraith *et al.* 2002; Iwamura *et al.* 2016; Lester *et al.* 2016). Eustatic sea level rise is predicted to have the greatest impact on terrestrial habitat in the tropical Pacific where terrestrial vertebrates are at risk of losing up to 22% of current habitable area to inundation (Wetzel *et al.* 2013). Not only will coastal habitat of this region be affected, but entire low-lying islands could be submerged (Wetzel *et al.* 2013; Bellard *et al.* 2014a). Owing to their tendency to occur in relatively low numbers on small, isolated islands, endemic landbirds are thought to be the most vulnerable (Jetz *et al.* 2007; Wetzel *et al.* 2013; Taylor & Kumar 2016). Some groups are particularly sensitive to the effects of climate change as a function of their habitat preferences, range and biology, and recent work has shown that the primarily mound-nesting megapodes are under particular threat (Chapter 2; Radley *et al.* 2018). One species that may be highly threatened by climate change, specifically sea level rise, is the endangered Micronesian Megapode of Palau (Radley *et al.* 2018). Although this subspecies also faces the potential cumulative anthropogenic challenges of tourism and introduced rats, very little is understood about its habitat needs in terms of breeding and foraging, a situation that may diminish effective conservation planning for it.

The Micronesian Megapode is a member of the family Megapodiidae, which is confined to the tropics and subtropics of the Indo-Pacific and Australasia where many species occur on relatively small and remote islands (Jones *et al.* 1995). Nineteen of the 22 species in the family construct mounds as at least one strategy for incubating their eggs (Jones *et al.* 1995). Unique to megapodes, none use body heat for incubation but instead employ other naturally occurring, environmental sources of heat (Jones *et al.* 1995). Mound building species specifically use heat generated by microbial decomposition of the fine organic matter from which their mounds are constructed (Jones *et al.* 1995). This organic matter consists of leaves and small woody debris that is collected directly from the forested habitat in which megapodes build their mounds (Jones *et al.* 1995; Sinclair 2002).

The majority of megapodes in Palau breed on the islands of the UNESCO World Heritage listed Rock Islands Southern Lagoon Conservation Area (RISL) (Wiles & Conry 2001; Olsen *et al.* 2016). Mounds in the RISL are commonly situated in strand forest, a salt-spray, wind, and wave resistant community of terrestrial forest vegetation that occurs along the coastal supratidal or littoral zones on many tropical islands, where

this forest type functions to stabilize tidal-zone soils and buffer island interior forests from storm surge (Keppel 2002; Whistler 2007). Mounds built in strand forest are generally placed in well-shaded sandy areas just above high tide and just inland from the beach; elevation is typically no more than a few meters above sea level (Wiles & Conry 2001; Olsen *et al.* 2013).

Areas of appropriate habitat in the RISL are limited and typically occur in relatively narrow strips of level and sandy littoral strand forest, which is generally sandwiched between beach and abrupt, near-vertical limestone hillsides (Pratt *et al.* 1980; Wiles & Conry 2001). On some comparatively larger islands, mounds may be located in more expansive areas of littoral strand habitat (Wiles & Conry 2001; Olsen *et al.* 2016). Mounds in this cover type were found to consist mainly of sand mixed with fine organic matter including leaves, twigs, roots, and needles of ironwood trees (*Casuarina equisetifolia*) (Wiles & Conry 2001; Olsen *et al.* 2013). Other species of megapodes in the tropics construct their mounds in locations where microhabitat characteristics both increase the availability of organic matter and provide microclimate stability, decreasing the rate of mound desiccation and maintaining optimal incubation temperatures within (Jones 1988; Sinclair 2002). Similarly, megapodes in the RISL would be expected to non-randomly select sites for mounds based on habitat and microclimate variables that increase incubation effectiveness and breeding success.

While few specifics are known about the habitat selected by Micronesian Megapodes for incubation sites (i.e., for mound building), even fewer are known about the habitat they use for foraging. This is a common gap in the research within the family with little published data pertaining to the use of habitat by megapodes away from incubation sites. What data are available regarding their foraging habitat tend to be relatively coarse in detail (e.g., Broome *et al.* 1984; Göth & Vogel 2003; Sivakumar & Sankaran 2012). Megapodes are generally omnivorous scratch-feeders and tend to range broadly through forested habitat opportunistically taking suitable food items as they uncover them (Jones *et al.* 1995). Regardless, the habitat they select for foraging can influence female fecundity and lead to overall greater reproductive output and, along with the habitat they choose for incubation sites, stimulate greater reproductive success (Jones *et al.* 1995; Sinclair 2002). Knowing the characteristics of habitat in the RISL that are important to megapodes, for both incubation sites and foraging, is essential for their long-term conservation.

Here I investigate what site- and habitat-specific variables are selected by megapodes in Palau, both when choosing incubation sites and while foraging in the RISL. I specifically hypothesized that megapodes in the RISL select incubation and foraging sites based on a structural component (or components) of habitat as opposed to forest / plant species composition. I predicted that areas of denser understory or canopy that a) produce more organic debris useful for mound building, and b) maintain a more stable external microclimate for mound incubation, would be preferred to areas that are less dense and simply dominated by a particular understory or canopy species. Similarly, I predicted that such areas of denser understory or canopy would provide denser and richer leaf litter that produced more invertebrate and plant food and would thus be selected for by foraging birds. I identify habitat variables that are the most important for the Micronesian Megapode in Palau and compare my findings to those for other species of megapodes that occur throughout the Indo-Pacific and Australasia.

Methods

Study Site

Palau (7° 30' N, 134° 35' E; Figure 3.1), the westernmost archipelago in Micronesia, is comprised of 12 inhabited islands and over 500 smaller islands and islets that extends ~700 km from northeast to southwest (Olsen 2009). Approximately 87 percent of the archipelago is forested, 75% of which is classified as native tropical lowland rainforest (Kitalong *et al.* 2013). My research focused exclusively on the islands of the RISL, which lies between Babeldaob to the northeast and Peleliu to the southwest (Figure 3.1). Unlike many other islands in the archipelago, these “rock islands” are ancient, uplifted reefs and thus coralline in nature (Engbring 1988). Most are uninhabitable by humans and characterized by sheer, highly fissured and eroded karst or limestone slopes that are undercut at the water’s edge and covered by dense forest despite little or no soil development beneath (Pratt *et al.* 1980; Engbring 1988). A number of these islands also exhibit fringing, sandy littoral zones where strand forest occurs on mostly level limestone soils immediately behind their beaches. This habitat, which falls under the

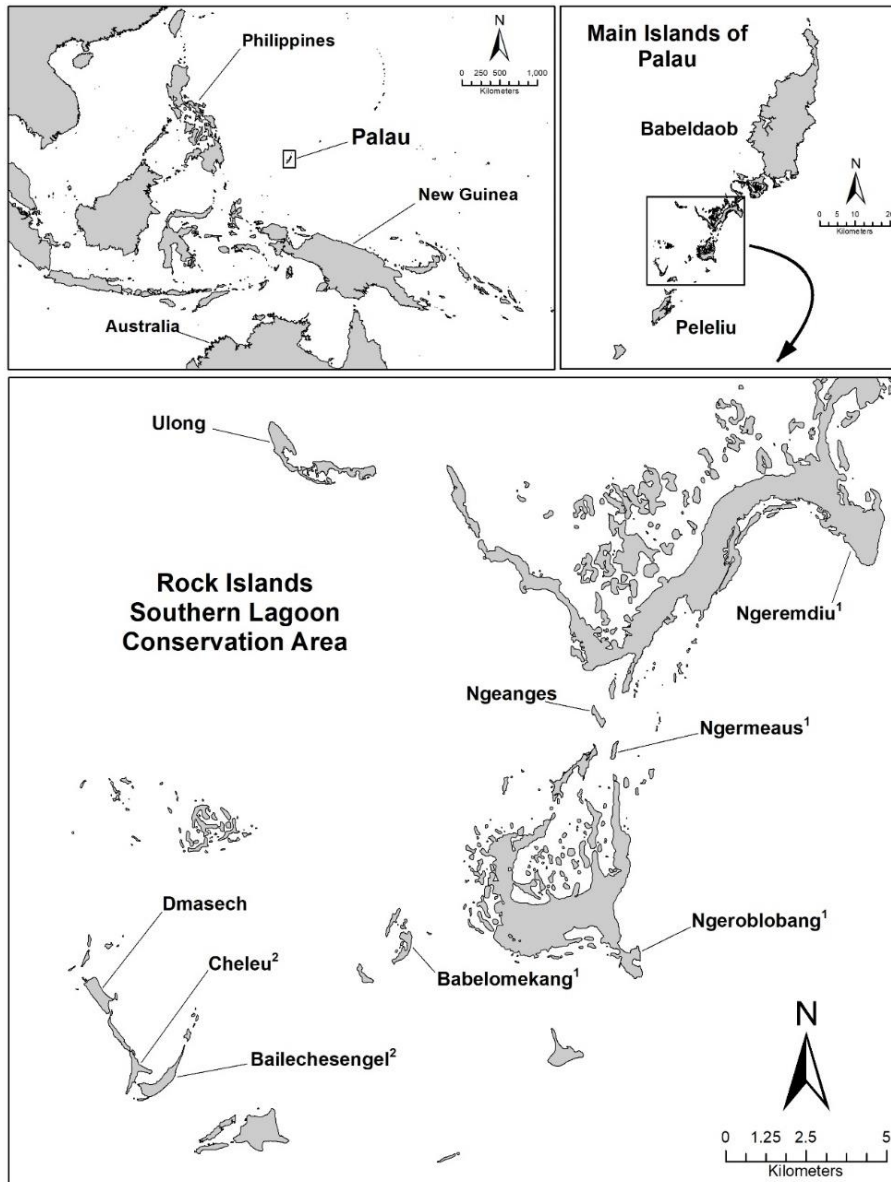


Figure 3. 1. Map of the study area within the Rock Islands Southern Lagoon Conservation Area (RISL) of Palau, and the locations of islands on which Micronesian Megapode habitat data were collected. A ¹ denotes those islands on which only breeding habitat data were collected, and a ² those on which only foraging habitat were collected. Both breeding and foraging habitat data were collected on the remaining three islands.

category of “Limestone Forest” (Kitalong *et al.* 2013), is that which megapodes almost exclusively prefer for breeding in the RISL (Olsen *et al.* 2016).

Incubation Mound Habitat Sampling

I collected habitat data at active megapode incubation mounds on seven islands from 19 February to 2 April 2016 and on 17 January 2017. Mounds were located either through use of a 2012 data set provided by Belau National Museum (pers. comm., A. Olsen), or by thorough search of littoral strand habitat on each island. Mound locations were acquired using a *Trimble Yuma* differential GPS (*Trimble Navigation Ltd.*, Sunnyvale, California, USA). I measured mound diameters and heights with a forester's tape measure, and distances of most from the shore (the furthest upper reach of high tide) with a handheld laser rangefinder. For those that lacked an unobstructed view to the shore I measured the distances with a forester's tape. If straight line distances were too great or blocked by impenetrable obstructions to accurately measure on-site, I determined necessary distances in ArcGIS (ESRI 2015).

I followed the methods of Sinclair (2002) for the measurement and collection of habitat data (Table 3.1). Habitat characteristics were assessed only at maintained and active incubation mounds. Mounds were considered active when they were obviously maintained and clear of heavy leaf, vine, fern or grass cover, were not worn flat or obviously eroded, and showed signs of megapode activity, or were obviously in a state of construction (Wiles & Conry 2001; Olsen *et al.* 2013). I did not include unmaintained or inactive mounds because my inability to reliably and accurately age them left me uncertain about the relative age of the surrounding forest. I also measured habitat variables at randomly selected sites (Table 3.1) for statistical comparison to those measured at mounds. All but two random sites were associated with active incubation mounds and were selected based on a table of random bearings and distances from mound centres, as generated in *Microsoft Excel* 2016. (The two additional random sites were associated with mounds at which I had collected data, but which I later determined to be inactive; I retained the data collected at the random sites for my analysis, regardless.) After completing data collection at a mound, I located its random site by choosing the next available pair of bearing and distance on the list and walked to it with the aid of compass and rangefinder or forestry tape measure. If these coordinates placed the random site in the ocean or on uplifted limestone, I chose the next available bearing and distance until it placed the random site in measurable habitat.

I measured and collected habitat data at mounds and random points at two

Table 3. 1. Habitat and site specific data collected at megapode incubation mounds, foraging plots, and corresponding randomly selected sites in the RISL of Palau. Under “Sample Location”, BA stands for “Base Area” (either the mound area or the random site center), SF stands for “Surrounding Forest” (i.e., the satellite plots at four cardinal directions around the BA), and FP for “Foraging Plot”.

Forest Habitat Variable	Sampling Method and (Unit)	Sample Location		
		BA	SF	FP
<i>Canopy and Understory</i>				
Tree dbh	DBH measuring tape (cm)	X	X	X
Number of seedlings	Stem count (< 4 cm DBH)	X	X	X
Number of saplings	Stem count (4-10 cm DBH)	X	X	X
Dominant species in above categories	Species name	X	X	X
Percent canopy cover	Aspherical densitometer, N, S, E, W (mean %)	X	X	X
Canopy height	Clinometer (degrees elevation)	X	-	-
No. of crowns in canopy	Visual count above plot centres	X	X	-
<i>Ground Cover</i>				
Proportion shrub cover	Visual estimate of coverage (%)	-	X	X
Proportion herb cover	Visual estimate of coverage (%)	-	X	X
Proportion of bare ground	Visual estimate of coverage (%)	-	X	X
Proportion of litter cover	Visual estimate of coverage (%)	-	X	X
Proportion of limestone cover	Visual estimate of coverage (%)	-	X	X
<i>Site Specific</i>				
Slope	Clinometer (degrees elevation)	X	-	-
Aspect (degrees from N)	Compass (degrees from N)	X	-	-
Mound distance to shore	Forester's tape (meters)	X	-	-

spatial scales: a ‘base area’ and the ‘surrounding forest’ (Sinclair 2002). Together, the base area and the surrounding forest constituted a sampling plot or ‘site’. The base areas consisted of everything within the mound perimeter, or a 3.5 m radius circle for random points. This radius was based on the mean diameter of 10 megapode mounds previously measured by Wiles and Conry (2001) in the RISL. Variables of the surrounding forest (which corresponded to the area where birds logically collect the majority of litter and soil for their mounds) were measured in four separate 2 m radius sampling plots, each established at the four cardinal directions around the base area.

The centres of these sampling plots were situated seven metres from the centre of the mound base area, thus providing 1.5 m of distance between the edge of the base area and the edge of each sampling plot. At mound sites, this compensated for any mounds with a radius slightly larger than the mean of 3.5 m and avoided overlap between the base area and any of its four surrounding forest sample plots.

Seven habitat variables were measured within the base area of both mound and corresponding random sites, 11 were measured in each surrounding forest and corresponding random sample plot, and three site specific variables were measured or assessed to describe each site as a whole (Table 3.1). I specifically selected variables that might exert some influence on the placement or function of mounds (Sinclair 2002). Diameter at Breast Height (DBH) was measured for all trees in base areas and sample plots and then placed in one of three life-stage categories: seedlings (all trees under 4 cm DBH), saplings (those between 4 and 10 cm DBH) and mature trees (those over 10 cm DBH). Mature trees and saplings were considered within and measured if they at least touched the perimeter of base areas or sample plots. Stem counts were recorded for all seedlings, along with the dominant species in all three categories. Seedling, sapling, and mature tree species were identified with either the aid of a printed field guide (Kitalong *et al.* 2013), the knowledge of my local field assistant (pers. comm., P. Terenciano), or by consulting the Belau National Museum's botanist (pers. comm., A. Kitalong). Dominant species were determined by quantifying the number of each species present for each life-stage category in sample plots. The species that occurred in highest number in each category was considered dominant. If there was no clear dominant species present within a category it was recorded as 'no dominant species'. Percent canopy cover was assessed with a spherical densitometer by averaging the readings at each of the four cardinal directions around the centres of each base area and at the centre of each surrounding forest sample plot. Canopy height was measured with a clinometer at base areas, and number of crowns in canopy was determined by the number of tree canopies that intersected or overlapped each 2 m radius plot boundary.

The proportion of all shrub, herb cover, and bare ground were assessed only in surrounding forest sample plots. Proportions were measured simply as the estimated percentage of each that covered the area within each plot. Although the ground cover on the mound itself indicated whether it was in active use, the ground cover variables

megapodes may have selected for when constructing their mounds obviously no longer existed as they would have been covered by the mound itself (Sinclair 2002). For consistency, ground cover variables within the base area of random sites were thus not measured.

Foraging Habitat Sampling

Megapode foraging habitat data were collected between 9 and 23 January 2017. I employed a modified version of ‘Instantaneous Sampling’ (e.g., O'Donnell & Dilks 1994), focusing specifically on measuring and quantifying the habitat in which megapodes foraged, as opposed to simply gathering standardized descriptive observations of habitat use. Observers (my assistant and I) walked slowly through littoral habitat using binoculars to scan ahead of them for megapodes. The uplifted limestone formations ubiquitous to the islands were not surveyed because the sheer nature of their slopes made them inaccessible in most cases. When a bird was observed, the behaviour it exhibited at first sight was recorded. If the individual bird did not obviously notice the observer, it was watched for foraging behaviour until it either became aware of the observer or until it moved out of sight. The observer then walked either to the location of first observation or to where the bird was seen actively foraging. For birds that were observed only momentarily prior to flushing or otherwise fleeing, the location of first visual observation became the centre point of the data collection plot. If birds were observed longer, the first observed location of actual foraging activity was used as the centre point.

Foraging habitat data were collected in the same manner as those at incubation mounds and many of the same variables were assessed and measured (Table 3.1). As megapodes tend to be generalist foragers (Jones *et al.* 1995), measurement of certain habitat variables was excluded to streamline collection of foraging data with the intent of increasing sample size. Ten habitat variables were measured within 1 m radius plots centred on both foraging locations and randomly chosen points (Table 3.1). Seedling stem counts, sapling and tree DBH measures, shrub, herb, and ground cover assessments all followed the methods described above for incubation mound data collection. Percent canopy cover was assessed with a spherical densitometer by

averaging the readings at each of the four cardinal directions around the centres of each foraging plot or randomly chosen point.

After completion of data collection at a given foraging site and its randomly chosen point, the observer moved towards the opposite end of the beach or island to search for another megapode from which to collect data. Although not quantified, the observers commenced data collection for a successive bird only if they were reasonably confident it was not the same one for which they had just completed foraging habitat measurements. This approach was taken to avoid successively collecting data for the same bird or pair, and to ensure the best possible independence between observations in the limited time that I had.

Data Analysis

For the purpose of analysis, all individual trees (≥ 11 cm DBH) were placed into four size classes: DBH of 11 to 30 cm; DBH of 31 to 50 cm; DBH of 51 to 70 cm; and DBH of > 70 cm. Prior to data normalization, I used two sample t-tests to investigate the significance of differences in individual habitat variables between mound base areas, surrounding forest, and foraging sites (collectively referred to here as “target sites”) and their corresponding random sites. The program PRIMER-E v6 with PERMANOVA add-on (Clarke & Gorley 2006) was then used for multivariate testing and display (via ordination) of the differences in overall habitat structure between target and random sites. All continuous habitat variables were first normalised and then Euclidean distances between sites were calculated. I then used a one-way Analysis of Similarities (ANOSIM, a non-metric test) and Permutational Multivariate Analysis of Variance (PERMANOVA, a metric approach: Anderson *et al.* 2008) to determine the significance level for difference between target and random sites. I used Non-metric Multi-Dimensional Scaling (MDS) and Principle Co-ordinates Analysis (PCO) to represent Euclidean distances between samples in two dimensions, the latter with vectors added showing significant Spearman rank correlations of habitat variables in the ordination space. Similarity percentages analysis (SIMPER) was then used in PRIMER-E to determine which habitat variables contribute to the top 90% of the overall Euclidean distance dissimilarity between target and random sites.

To investigate the importance of dominant tree species to megapodes for selection of incubation and foraging sites, I used chi-squared tests in SPSS to test for the differences in the frequency of dominant species of mature trees, saplings, and seedlings between target sites and random sites. Given the low counts or null values for species in some of these life-stage categories, I used Fisher's Exact Test with Monte Carlo estimation to determine significance.

Results

Mound Habitat

I collected habitat data at 24 incubation mounds and 26 randomly chosen sites on seven islands within the RISL (Figurer 3.1). (As discussed above on page 31, the additional two random sites were associated with mounds I had at first thought to be active.)

These 24 mounds represent all known active mounds on these islands, to which my time was restricted for mound habitat assessment (Appendix A) at the time of data collection. Specifically, 19 were active or maintained and the remaining five mounds were in the process of being constructed. Mound diameters ranged from 3.5 m to 9.6 m (\bar{x} = 6.7 m) and only three mounds were situated on substrate that exhibited any sort of relief with relatively gentle slopes of 3°, 5°, and 15°, and slope aspects of 70°, 218°, and 115°, respectively. From comparison of individual habitat variables between mound base areas and random sites with two sample t-tests, I found four variables that were significantly different ($P < 0.05$) between mound base areas and random (Table 3.2). Mounds were constructed closer to shore (range = 5–136 m) than random sites (range = 11–167 m), and mound base areas contained fewer trees in size class 31–50 cm DBH than random (Table 3.2). Reflecting the fact that 20 of the 24 mounds studied were constructed at the base of large trees, base areas also contained more trees over 70 cm DBH and exhibited significantly greater canopy height than random sites (Table 3.2). Eleven (45%) of these large trees were ironwood, one of which was a snag that had been “strangled” by a *Ficus* sp. Four (17%) other mounds were constructed at the base of large breadfruit trees (*Atrocarpus mariannensis*) and three (13%) were at the base of large snags or stumps that were in the later stages of decay and were identified as unknown species. The remaining two mounds were constructed at the bases of a coral (*Erythrina fusca*) and Indian beech (*Milletta pinnata*)

Table 3. 2. Means (\pm SD) of untransformed data for habitat variables collected at megapode mound base areas (BA), surrounding forest (SF) at mounds, megapode foraging plots (FP), and all associated random sites in the Rock Island Southern Lagoon Conservation Area (RISL), Palau.

Habitat Variables	BA Mound (<i>n</i> = 24)	BA Random (<i>n</i> = 26)	SF Mound (<i>n</i> = 24)	SF Random (<i>n</i> = 26)	FP Site (<i>n</i> = 62)	FP Random (<i>n</i> = 62)
No. of Seedlings	28.8 \pm 43.6	36.3 \pm 29.2	68.2 \pm 61.7	70.4 \pm 48.9	8.8 \pm 8.3	10.2 \pm 11.1
No. of Saplings	1.5 \pm 1.5	2.3 \pm 2.5	2.7 \pm 2.4	4.5 \pm 4.4	0.4 \pm 0.8	0.3 \pm 0.6
Trees 11 to 30 cm DBH	1.6 \pm 1.7	0.8 \pm 1.4	2.0 \pm 1.9	1.9 \pm 1.7	0.1 \pm 0.3	0.2 \pm 0.4
Trees 31 to 50 cm DBH	0.08 \pm 0.3**	0.5 \pm 0.7	0.6 \pm 1.2	0.6 \pm 0.9	0.1 \pm 0.4	0.1 \pm 0.3
Trees 51 to 70 cm DBH	0.08 \pm 0.3	0.1 \pm 0.4	0.04 \pm 0.2	0.1 \pm 0.3	-	-
Trees > 70 cm DBH	0.8 \pm 0.6*	0.1 \pm 0.3	0.1 \pm 0.3	0.1 \pm 0.3	-	-
% Canopy Cover	96.6 \pm 2.3	97.2 \pm 2.9	96.3 \pm 2.6	96.3 \pm 4.2	97.1 \pm 2.1	96.6 \pm 3.6
Canopy Height	26.0 \pm 8.1*	19.2 \pm 7.1	-	-	-	-
No. of Crowns	2.1 \pm 0.9	2.4 \pm 1.2	1.7 \pm 0.3	1.6 \pm 0.6	-	-
% Shrub Cover	-	-	0.1 \pm 0.5	0.3 \pm 1.0	-	-
% Herb Cover	-	-	9.5 \pm 13.1	12.1 \pm 13.9	6.8 \pm 13.7	9.9 \pm 19.2
% Bare Ground	-	-	22.6 \pm 21.5	18.5 \pm 16.9	37.9 \pm 28.8	33.9 \pm 27.9
% Litter Cover	-	-	77.0 \pm 21.3	77.9 \pm 20.8	56.2 \pm 29.9	60.9 \pm 29.8
% Limestone Cover	-	-	0.4 \pm 2.0	3.9 \pm 16.5	5.5 \pm 16.8	3.7 \pm 12.0
Distance to Shore	41.9 \pm 27.7**	61.8 \pm 40.6	-	-	-	-
% Slope	0.9 \pm 3.2	1.3 \pm 2.6	-	-	-	-
Slope Aspect	16.8 \pm 50.6	40.7 \pm 81.6	-	-	-	-

* Significantly different for $P = 0.05$ to 0.01

** Significantly different for $P < 0.01$

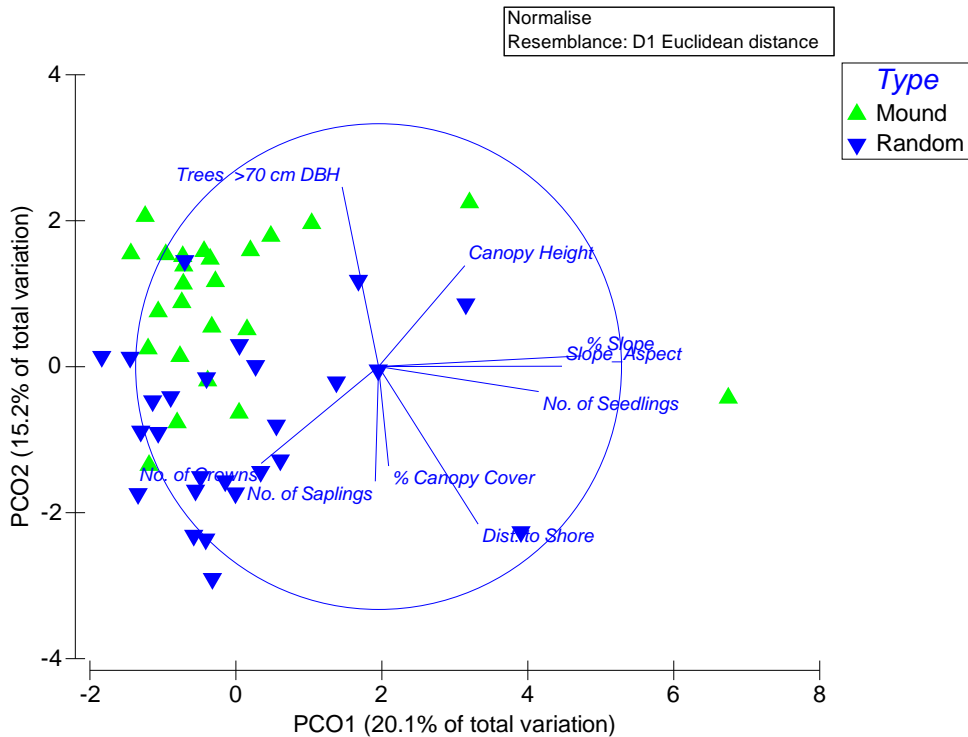


Figure 3. 2. Results of Principle Co-ordinates Analysis (PCO) for megapode mound base areas as compared to random sites in the Rock Islands Southern Lagoon Conservation Area (RISL), Palau. Only variables with a Pearson Correlation of > 0.40 are included in the graph and length of the generated line is proportional to the strength of the correlation.

tree. T-tests revealed no significant difference ($P > 0.05$) between individual habitat variables at surrounding forest sample plots compared to their random sites (Table 3.2).

My ANOSIM comparing mound base areas and random sites yielded a significant ($P < 0.001$) difference in habitat variables between these two groups (Global $R = 0.131$), and a distance-based multivariate test (PERMANOVA) further supported the significance of this difference (Pseudo- $F = 3.85$, $P < 0.001$). Although there is some overlap in the ordination space, the general separation of sites can be seen in my PCO (Figure 3.2). Vectors (Spearman correlations) in the PCO (Figure 3.2) indicate that the variables of trees over 70 cm DBH, distance to shore, and to a lesser extent canopy height and the number of crowns, were the most strongly correlated and played the largest role in explaining the difference between mound base areas and random sites. The SIMPER analysis further supported this and indicated that trees over 70 cm DBH and canopy height contribute to the top 19.5% of Euclidian distance dissimilarity

Table 3. 3. Results of Similarity Percentages Analysis (SIMPER) indicating which habitat variables contribute to the top 90% of the overall Euclidian distance dissimilarity between megapode mound base areas and random sites in the Rock Island Southern Lagoon Conservation Area (RISL), Palau.

Habitat Variable	Average Values at Sites		Av. Sq. Distance	SD	Percent Contribution	Cumulative Percentage
	Mound	Random				
<i>Mound Base Area vs. Random</i>						
DBH \geq 71	0.574	− 0.53	2.60	0.86	10.33	10.33
Canopy Height	0.424	− 0.392	2.30	0.81	9.14	19.47
DBH of 31 to 50	− 0.398	0.368	2.21	0.63	8.77	28.24
DBH of 11 to 30	0.258	− 0.239	2.10	0.58	8.34	36.58
Distance to Shore	− 0.287	0.265	2.09	0.67	8.28	44.87
No. of Seedlings	− 0.107	9.85E-2	2.01	0.47	7.99	52.85
No. of Saplings	− 0.213	0.197	2.01	0.70	7.98	60.83
No. of Crowns	− 0.156	0.144	1.99	0.80	7.91	68.74
Slope Aspect	− 0.17	0.157	1.99	0.47	7.89	76.64
% Slope	− 5.59E-2	5.16E-2	1.98	0.38	7.87	84.50
% Canopy Cover	− 0.118	0.109	1.97	0.52	7.82	92.32

between mound base areas and random (Table 3.3), and both these variables were significantly more prominent at base areas (Tables 3.2). SIMPER analysis also indicated that trees with DBH of 11 to 30 cm were more prominent at base areas, while those with a DBH of 31 to 50 cm were significantly less prominent (Tables 3.2 and 3.3). Although random sites contained more seedlings and saplings, and were covered by more tree crowns and a denser canopy (Table 3.3), t-tests suggested that none of these variables were significantly different from base areas (Tables 3.2). Random sites were, however, situated significantly farther from shore than mound base areas (Tables 3.2 and 3.3). An ANOSIM comparing surrounding forest at mounds to random sites indicated no significant difference between these two groups (Global $R = -0.019$, $P = 0.844$), which was further supported by the MDS (Figure 3.3).

I identified 22 species of seedlings, saplings and mature trees as dominant at mound base areas and their surrounding forest plots, compared to 17 species identified as dominant at corresponding random sites (Table 3.4 and 3.5). The frequency of site species dominance was significantly different between mound base areas and random sites for trees only ($X^2 = 21.21$, $P = 0.020$; Table 3.4). No other tree life-stage category

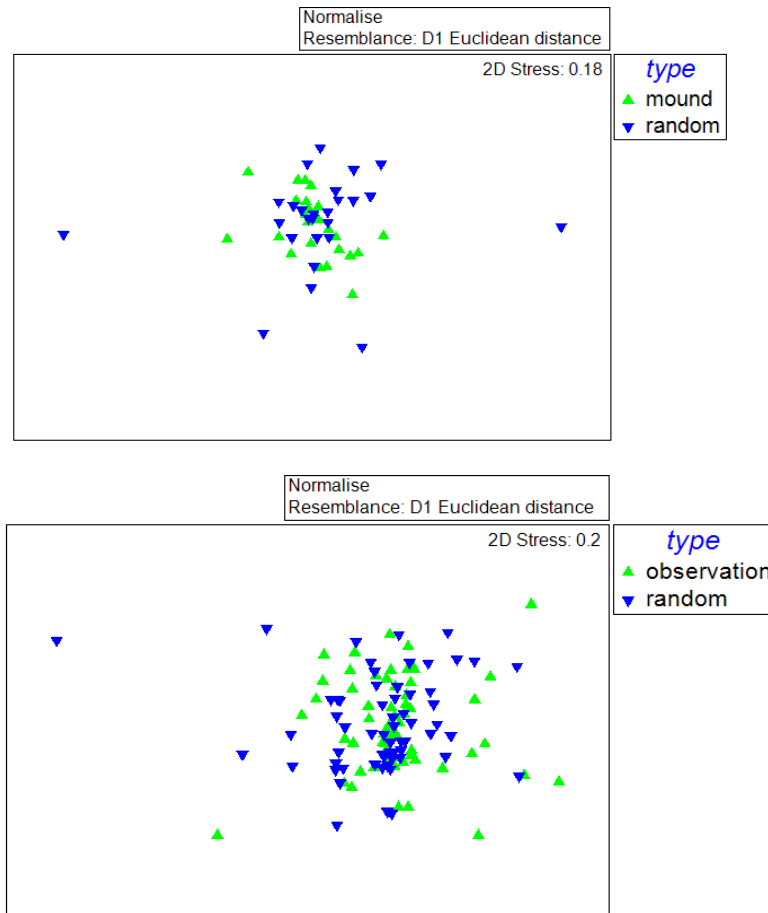


Figure 3. 3. Results of Non-metric Multi-Dimensional Scaling (MDS) for surrounding forest sample plots at mounds (top) and megapode foraging sites (bottom), as compared to their random sites.

in base areas and random sites and no category in surrounding forests sites and random sites showed a significant difference in species dominance ($P > 0.05$; Table 3.4). Of the two mature tree species that occurred at both mound base areas and random sites, Coconut palm (*Cocos nucifera*) and Java-apple (*Syzygium samarangenses*) were more likely to be dominant at the latter, while breadfruit was more likely dominant at the former. Forty-six percent of base areas contained no dominant species compared to 11% of random sites, a difference which is significant ($X^2 = 5.29$, $DF = 1$, $P = 0.021$). This difference also drove the overall difference between mound base areas and random sites as reported above, with base areas much less likely to exhibit a clear dominant species compared to the surrounding forest.

Table 3. 4. Percentages of dominant species of seedlings, saplings, and mature trees at mound base areas (BA) compared to random sites (R) in the Rock Islands Southern Lagoon Conservation Area (RISL) of Palau. Fourteen species total between the three categories were identified at both base areas and random sites. The χ^2 statistic (from Fisher's Exact Test with Monte Carlo estimation) comparing the frequency distribution of dominant species between base area and random is in parenthesis for each plant category.

Seedling ($\chi^2 = 13.81$, df = 12, P = 0.211)		Sapling ($\chi^2 = 8.99$, df = 12, P = 0.867)		Mature Tree ($\chi^2 = 21.21$, df = 15, P = 0.020)	
	BA% R%		BA% R%		BA% R%
No Dominant Species	13 30	No Dominant Species	17 15	No Dominant Species	46 11
No Seedlings	8 -	No Saplings	42 30	No Trees	17 19
<i>Barringtonia asiatica</i>	4 -	<i>Carica papaya</i>	4 -	<i>Atrocarpus mariannensis</i>	13 -
<i>Calophyllum inophyllum</i>	4 4	<i>Cocos nucifera</i>	4 4	<i>Averrhoa bilimbi</i>	- 4
<i>Cocos nucifera</i>	13 18	<i>Horsfieldia palauensis</i>	- 8	<i>Calophyllum inophyllum</i>	- 4
<i>Hernandia nymphaeifolia</i>	8 4	<i>Ixora casei</i>	- 4	<i>Carica papaya</i>	- 4
<i>Horsfieldia palauensis</i>	- 12	<i>Macaranga carolinensis</i>	4 -	<i>Casuarina equisetifolia</i>	4 -
<i>Inocarpus fagifer</i>	- 4	<i>Milletta pinnata</i>	4 -	<i>Cocos nucifera</i>	8 19
<i>Ixora casei</i>	- 4	<i>Morinda</i> sp.	4 4	<i>Horsfieldia palauensis</i>	- 4
<i>Milletta pinnata</i>	4 -	<i>Ochrosia oppositifolia</i>	13 12	<i>Inocarpus fagifer</i>	- 4
<i>Ochrosia oppositifolia</i>	29 12	<i>Osmoxylon</i> sp.	- 4	<i>Milletta pinnata</i>	4 -
<i>Syzygium samarangense</i>	13 12	<i>Polyscias</i> sp.	4 4	<i>Morinda</i> sp.	- 4
Unknown	4 -	<i>Syzygium samarangense</i>	4 15	<i>Ochrosia oppositifolia</i>	- 4
				<i>Syzygium samarangense</i>	4 19
				<i>Terminalia catappa</i>	4 -
				<i>Timonius timon</i>	- 4

Table 3. 6. Percentages of dominant species of seedlings, saplings and mature trees at foraging plots (FP) and associated random plots (R) in the Rock Islands Southern Lagoon Conservation Area (RISL), Palau. Thirteen species total between the three categories were identified at foraging plots, while random sites comprised 18 species. The χ^2 statistic (from Fisher's Exact Test with Monte Carlo estimation) comparing the frequency distribution of dominant species between foraging plots and random is in parenthesis for each plant category.

Seedling ($\chi^2 = 12.09$, df = 15, P = 0.713)			Sapling ($\chi^2 = 15.02$, df = 15, P = 0.053)			Mature Tree ($\chi^2 = 13.79$, df = 15, P = 0.540)		
	FP%	R%		FP%	R%		FP%	R%
No Dominant Species	10	10	No Dominant Species	-	-	No Dominant Species	2	-
No Seedlings	8	7	No Saplings	76	82	No Trees	77	68
<i>Apocyanaceae</i> sp.	1	-	<i>Averrhoa</i> sp.	-	1	<i>Ambrosia</i> sp.	-	3
<i>Artocarpus mariannensis</i>	-	1	<i>Barringtonia asiatica</i>	3	-	<i>Averrhoa</i> sp.	-	2
<i>Barringtonia asiatica</i>	7	3	<i>Calophyllum inophyllum</i>	1	2	<i>Barringtonia asiatica</i>	1	-
<i>Calophyllum inophyllum</i>	10	7	<i>Draceana multiflora</i>	-	1	<i>Casuarina equisetifolia</i>	-	2
<i>Cocos nucifera</i>	5	10	<i>Hernandia</i> sp.	1	-	<i>Cocos nucifera</i>	7	11
<i>Ficus</i> sp.	7	3	<i>Horsfeldia</i> sp.	10	2	<i>Cordia</i> sp.	1	-
<i>Hernandia</i> sp.	3	3	<i>Ochrosia oppositifolia</i>	-	7	<i>Hernandia</i> sp.	5	-
<i>Horsfeldia</i> sp.	19	10	<i>Pandanus</i> sp.	-	2	<i>Horsfeldia</i> sp.	-	5
<i>Morinda</i> sp.	1	3	<i>Syzygium samarangense</i>	2	-	<i>Macaranga</i> sp.	-	1
<i>Ochrosia oppositifolia</i>	10	16	<i>Terminalia</i> sp.	2	-	<i>Morinda</i> sp.	-	1
<i>Pandanus</i> sp.	1	-	Unknown	5	3	<i>Ochrosia oppositifolia</i>	-	2
<i>Polyscias</i> sp.	-	1				<i>Pandanus</i> sp.	3	-
<i>Syzygium samarangense</i>	18	25				<i>Syzygium samarangense</i>	2	2
Unknown	-	3				Unknown	2	3

Foraging Habitat

I collected microhabitat data at 62 megapode foraging sites and 62 randomly chosen sites on five islands in the RISL (Figure 3.1). T-tests yielded no significant difference ($P > 0.05$) in individual habitat variables between these two groups (Table 3.2). An ANOSIM likewise yielded no significant difference between these two groups (Global $R = -0.007$, $P = 0.804$) and this was further confirmed by MDS (Figure 3.3).

I identified 13 species of seedlings, saplings and mature trees as dominant at megapode foraging sites, while 18 species were identified as dominant at corresponding random sites (Table 3.6). There was no significant difference ($P > 0.05$) in the frequency of species dominance of seedlings, saplings or mature trees between foraging or random sites (Table 3.6).

Discussion

Habitat at Mounds

Micronesian Megapodes in the RISL preferentially selected incubation sites that were relatively close to shore, contained large trees, and exhibited greater canopy heights than the surrounding forest. This preference for large trees and high forest canopies at mounds is consistent with findings for populations of the Wattled Brush-turkey (*Aepypodius arfakianus*), Brown-collared Talegalla (*Talegalla jobiensis*) and New Guinea Megapode in the eastern highlands of New Guinea (Sinclair 2002), the Philippine Megapode (*Megapodius cumingii*) in northern Sulawesi (Sinclair *et al.* 2002), and the Australian Brush-turkey (*Alectura lathami*) in southeast Queensland (Jones 1988). Both Jones (1988) and Sinclair (2002) suggested that incubation sites in Queensland and New Guinea, respectively, were selected based on the presence of large trees, the latter postulating that they provide more organic litter and microclimate enhancing shade for proper mound function, and that they may serve as a base against which mounds can be supported while being built. Forty-five percent of the active megapode mounds in the RISL from which I collected habitat data were constructed at the base of large ironwood trees, a salt-tolerant species of tree native to Southeast Asia and the Western Pacific, which is generally confined to sandy coastal areas and is a common component of littoral strand habitat throughout the region (Orwa *et al.* 2009).

In terms of the megapode breeding habitat assessed in my study, this species of tree was only present at mound base areas (Table 3.4), a factor that strongly contributed to the overall higher canopies at mounds.

As part of my investigation for Chapter 4, I collected GPS locations of 198 active, inactive, and mounds under construction in the RISL (including those in my analysis here), 30% ($n = 59$) of which were built at the base of moderate to large trees; 64% ($n = 38$) of these were identified as ironwood. In most instances during surveys, this species was the largest and most prominent tree in the strand forests of the RISL, with DBH measures of well over 100 cm (pers. obs., P. Radley). In a previous study of megapode mounds in Palau, Wiles and Conry (2001) found that 10 of 12 active mounds in strand habitat were constructed at the base of relatively large trees, the most common of which was lantern tree (*Hernandia nymphaeifolia*) followed by ironwood. This difference may in part be attributed to the fact that much of their data were collected either outside of the RISL or in the highly restricted Ngerukuid Islands Wildlife Preserve (Wiles & Conry 2001), to which I was not permitted access.

Other studies of mound building megapodes have determined that a denser or more closed canopy is a significant factor in the selection of incubation sites (Jones 1988; Sinclair 2002). While forest canopy at mound base areas in the RISL approached 100% coverage, canopies at mounds were not significantly denser or more closed than random. Canopy cover across all target and random sites in my study (i.e., from 224 data collection points across nine islands) yielded a mean for each that ranged from 96.3 – 97.2% (Table 3.2). This strongly suggests that canopy cover of the littoral strand forests in the RISL are uniformly dense and closed, and evenly suitable for mound incubation throughout in terms of microclimate maintenance and enhancement of conditions favourable to vegetative decomposition (Sinclair 2002).

Studies by Jones (1988) and Sinclair (2002) showed that other species of megapodes selected incubation sites based specifically on habitat features of the surrounding forest that both increased the availability of organic matter for mound construction and moderated sub-canopy microclimate, which prevents mounds from desiccating. There were no significant differences, however, in habitat variables between forest immediately surrounding mound base areas and random sites in my study. This suggests that megapodes in the RISL do not necessarily select incubation

sites based on the presence of readily available leaf litter and fine organic matter to provision their mounds. Considering the evenly dense, closed canopy over the vast majority of their preferred breeding habitat throughout the RISL, the availability of ‘fuel’ for incubation may not be a driving concern for the species. Instead, my data suggest that they choose sites based on specific variables pertaining to where the mound itself will be placed. The significantly lower density of medium-sized trees (31 to 50 cm DBH) within base areas could be a function of the distances that trees of this and larger size classes may naturally distribute themselves in proximity to the very large trees the majority of mounds were built around. Although my analysis found them not significant, a greater density of smaller DBH (11 to 30 cm size class, $\bar{x} = 18.6$ cm) and thus generally lower stature trees at base areas may provide a denser forest sub-canopy that helps maintain a moister microclimate closer to the mound at ground level.

Nearly half of all mound base areas at which I measured habitat in the RISL lacked a species of dominant tree (Table 3.4). My results showed that base areas were more likely to exhibit a mix of tree species with no clear dominant present. A more mixed selection of tree species may provide a more diverse variety of organic matter for mound construction. As megapodes in Palau may breed year-round (Jones *et al.* 1995), this may also ensure the availability of material for maintenance throughout the year. Regardless of the fact that the majority of megapodes apparently chose ironwood when selecting a tree around which to build their mounds, this tree species was dominant at only one base area. Although my results do suggest that megapodes choose sites based on the presences of breadfruit, this tree species was present at only four base areas and in all cases it had been selected specifically for mounds to be constructed against. Perhaps more notable, birds in the RISL may have selected incubation sites that lacked or were not in the immediate vicinity of mature coconut palms. Jones (1988) found that Australian Brush-turkeys specifically avoided dense areas of eucalypts (*Eucalyptus sp.*) when choosing incubation sites, likely owing to the decomposition resistant properties of their leaves. The older fallen fronds of coconut palms are large, relatively heavy, and may be challenging for megapodes to move, perhaps leading them to simply select incubation sites that are free of fallen fronds and, consequently, coconut palms. While not specifically a study of habitat use but rather an analysis of species density and abundance by habitat cover type, Amidon *et al.* (2011) found abundances of Micronesian Megapodes (*M. l. laperouse*) in the Mariana Islands to be greater in

coconut dominated forests compared to native forests. These reported differences, however, were not statistically significant and their study did not necessarily concern breeding birds but pertained to all detected individuals. While Java-apple was likewise significantly avoided by megapodes in the RISL, this species was the second most common tree at or within mounds of Nicobar Megapodes (*Megapodius nicobariensis*), following *Pandanus* (Sivakumar & Sankaran 2012).

Foraging Habitat

In terms of structure and species composition, my results indicate that megapodes in the RISL foraged in a non-preferential manner, apparently making use of all littoral strand forest habitat. Although not significant, my data suggest that birds tend to forage under dense canopy cover in open locations away from trees and saplings and with sparse herb cover, yet relatively dense in seedlings and with a moderate litter cover approaching 60% (Table 3.2 & 3.6). While anecdotally this description is suitable for much of the littoral areas where megapodes forage in the RISL, the apparent lack of saplings and trees may in part be a result of my sampling method. I measured all habitat variables within 1 m radius plots centred on the observed location of megapodes, either where birds were seen to be actively foraging or where they were first seen prior to being flushed. In the latter case, I assumed birds had been foraging prior to being flushed. Although not quantified, often times saplings and trees were within relative close proximity to foraging locations, but not close enough to fall within the relatively small radius of the sample plot. Given this, I suggest that the random sites associated with mound base areas and surrounding forest plots may more accurately reflect the structural make-up of the forests in which megapodes forage.

There are relatively few studies that focus on the use of habitat by megapodes outside of that which they require for breeding. Broome *et al.* (1984) found that the Melanesian Megapode (*Megapodius eremita*) dispersed to lowland rainforest in Western New Britain during the non-breeding season. While this cover type constitutes their primary foraging habitat, Melanesian Megapodes also made light use of swamp and hill forests and areas of garden regrowth (Broome *et al.* 1984). Although their study did not explicitly consider foraging habitat use of the Nicobar Megapode, Sivakumar and Sankaran (2012) observed the majority of species in cover types of

pagoda tree (*Clerodendrum peniculatum*) and *Pandanus* and found that they preferred microhabitats dominated by *Pandanus* and kenda (*Macaranga peltata*), regardless of season. Most Nicobar Megapodes were also observed during the non-breeding season in sandy-loam substrates, which Sivakumar and Sankaran (2012) hypothesized was because it may have been richer in invertebrate food resources than the strictly sandy substrate on which the species constructs its mounds. Like all other megapodes, the Micronesian Megapode in the RISL is omnivorous, consuming various small invertebrates and arthropods, snails, larvae, seeds, small fruits and other plant matter (Jones *et al.* 1995). This generalist feeding behaviour might be reflected in their non-specific use of foraging habitat.

I feel that the modified form of instantaneous sampling I employed was appropriate and adequate for my assessment of foraging habitat use by megapodes in the RISL. I do suggest, however, that measuring variables in 2 m radius sampling plots may better capture a truer representation of the habitat in which they forage by potentially including more saplings and trees in samples. Larger sampling plots, and counting the number of crowns above their centres, would also have made possible a direct comparison with the habitat variables collected at sample plots in the surrounding forest at incubation mounds. This would allow for a more accurate and informative assessment of the overall structure of littoral forest in the RISL, and perhaps allowed for a more nuanced assessment of the use of this cover type for foraging by megapodes.

Sea Level Rise and Conservation Implications for Megapodes in the RISL

The RISL was designated by UNESCO as a World Heritage Site in 2012 (Reepmeyer *et al.* 2011) and, being one of the world's foremost SCUBA diving destinations, is Palau's primary tourist attraction (IMF 2016). Additional to its UNESCO-listed status, the RISL is an official Palau government conservation area, and forested habitat is therefore not directly threatened by serious, destructive anthropogenic activities such as deforestation resulting from industrial logging or agriculture, the primary conservation threat to the majority of the world's megapodes (Jones *et al.* 1995; Dekker *et al.* 2000; IUCN 2016). The local Koror State Government Rangers, however, brush cut and clear low stature understory vegetation (primarily herbs and small woody plants, seedlings, and smaller saplings) on some beaches that are preferred as picnic and rest spots by dive

companies to make them more attractive to tourists (pers. comm., A. Kitalong; pers. obs., P. Radley). Such beach areas are far more exposed to wind and direct sunlight, are noticeably warmer and drier than undisturbed, thickly vegetated beach areas, and as a result may be less preferred by megapodes as incubation sites. Birds were readily seen foraging at some of these beaches, often amongst the very shelters and structures erected for use by tourists.

Although human-caused habitat loss may not be a major threat to megapodes in the RISL, climate change driven sea level rise could have serious implications for their breeding by the end of the current century. The strand forest habitat that megapodes rely on for incubation sites is vulnerable to future scenarios of eustatic rise predicted by the Intergovernmental Panel for Climate Change (IPCC) (Church *et al.* 2013; Radley *et al.* 2018). Terrestrial vertebrate species of Oceania may be the most impacted by rising seas and are predicted to lose up to nearly a quarter of their current ranges (Wetzel *et al.* 2013). Landbirds throughout this region may be at particular risk given their tendency to occur on small, remote Pacific islands (Wetzel *et al.* 2013; Taylor & Kumar 2016). The megapode in my study non-randomly selected low lying incubation sites that were located on average 42 meters from shore (Table 3.2), and the vast majority of mounds are within close proximity to sea level at high tide (Olsen *et al.* 2013; Olsen *et al.* 2016). Wiles and Conry (2001) previously reported distances of 5–15 m from shore for eight megapode mounds in the RISL, but these all occurred on narrow beaches compared to many that I surveyed for my study.

The Nicobar Megapode is the only other mound nesting species that usually chooses coastal forest incubation sites on well drained, sandy soils that are close to shore, the vast majority of which are within 100 m of the beach (Sankaran 1995; Sivakumar & Sankaran 2012). This species, however, has the option of establishing incubation sites further from the shore and has been recorded doing so with mounds documented as far as 15 km inland on Grand Nicobar Island (Sankaran 1995). Micronesian Megapodes that may breed on small outlying islands just off the larger island of Babeldaob (Figure 3.1) may similarly have this option, but the status of the species both occurring and breeding on this island requires further study and confirmation (pers. comm., A. Olsen; Olsen & Eberdong 2012). While megapodes in the RISL may have the opportunity to forage in the higher limestone areas, the option of selecting breeding habitat in strand forest at a safer distance from the ocean does not

exist within the conservation area. On the island of Dmasech in the Ngemelis Complex (Figure 3.1.), for example, I documented one mound at 136 m from the shore, representing nearly the farthest from the water a megapode can establish an incubation site in known suitable habitat in the RISL. The 2004 Indian Ocean tsunami devastated the Nicobar Islands and greatly impacted megapode populations, extirpating the species from two islands, and decreasing coastal breeding habitat by about 60% (Sivakumar 2010). Aside from sea level rise, similar abrupt stochastic events in the form of storm surges associated with increased storm intensity and frequency that are predicted as a part of climate change could pose at least equally serious consequences for megapodes in the RISL.

My findings suggest that the Micronesian Megapode in Palau has broad preferences in terms of foraging habitat, which is likely a reflection of its broad and non-specialized diet (Jones *et al.* 1995). This species does, however, specifically select locations to construct their mounds that contain large trees with DBH exceeding 70 cm, which provide high canopy cover, and that are situated relatively close to shore. My findings help to further characterize and identify necessary or ‘critical habitat’ for the Micronesian Megapode in Palau, and will help to inform modelling exercises that are intended to measure the effects of climate change driven sea level rise on the subspecies in the archipelago and other island restricted species.

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CHAPTER 4: Effect of predicted Sea Level Rise on Micronesian Megapode Breeding Habitat in the Rock Island Southern Lagoon, Palau

This chapter is not included in this version of the thesis.

CHAPTER 5: Assessing the Effects of Introduced Rats and Tourism on Micronesian Megapodes in the Rock Islands Southern Lagoon Conservation Area, Palau

Radley, P.M., R.A. Davis, and T.S. Doherty. (in review). *Effects of Introduced Rats and Tourism on a Threatened Island Bird*. Bird Conservation International XX: XX-XX

Introduction

In Chapter 4, I assessed the effect of three projected sea level rise scenarios on the Micronesian Megapode (*Megapodius laperouse senex*) in the RISL of Palau. While they breed in less than five percent of forest cover in the RISL, I determined that this population of megapode will be at least moderately impacted by sea level rise as predicted by 2100. The presences of rats and tourists in the RISL could serve as serious added stressors to the megapode, a species whose breeding habitat is currently threatened by climate change driven sea level rise.

Invasive predators are a leading cause of biodiversity loss on islands worldwide, having contributed to more than 50% of bird, mammal and reptile extinctions (Doherty *et al.* 2016). Rats (*Rattus* spp.) are perhaps the most successful invasive predator and are established on approximately 80–90% of islands globally (Towns *et al.* 2006). Occurring on 78% of islands known to support highly threatened vertebrates (Spatz *et al.* 2017), rats are well documented to be exceedingly detrimental to island avifauna (e.g., Courchamp *et al.* 2003; Towns *et al.* 2006; Tabak *et al.* 2014; Harper & Bunbury 2015). For instance, between Taukihepa and Lord Howe Islands in the South Pacific alone, the ubiquitous black rat *R. rattus* is responsible for the extinction of 10 native and endemic species of birds (Towns *et al.* 2006; Shiels *et al.* 2013).

The Micronesian Megapode is a species of ground nesting bird that occurs in the Mariana and Palau archipelagos of western Micronesia (Jones *et al.* 1995). A member of the family Megapodiidae, they do not incubate their eggs with body heat but instead employ external, environmental sources of heat (Jones *et al.* 1995). The subspecies of

megapode in Palau (*M. l. senex*) buries its eggs in large mounds of sand filled with decomposing organic matter, which it constructs predominantly in littoral strand forest that occurs throughout portions of the archipelago (Wiles & Conry 2001; Olsen *et al.* 2016). The largest segment of this population is found in the UNESCO World Heritage listed Rock Islands Southern Lagoon Conservation Area (RISL) (Olsen *et al.* 2016).

Citing a small, fragmented distribution, comparatively small population size, and its continued decline, the IUCN (2016) classifies the Micronesian Megapode as Endangered. Documented and potential threats to the species are mostly, but not wholly, deterministic in nature and include hunting, egg collecting for human consumption, and introduced predators (Pratt *et al.* 1980; USFWS 1998; IUCN 2016). Sources suggest that introduced rats are a direct threat to megapodes in both the Mariana and Palau archipelagos, but none cite any direct, quantitative evidence as justification (USFWS 1998; Wiles & Conry 2001; Olsen *et al.* 2013). Four species of rat have become established in Palau, two of which—the Polynesian rat *R. exulans* and black rat—occur in forested areas of the RISL (Wiles & Conry 1990) and may be detrimental to megapodes. Although no other species of megapode is known or believed to be threatened by rats (IUCN 2016), populations of some ground and burrow nesting seabirds have been seriously affected (Jones *et al.* 2008; Ruffino *et al.* 2009).

Aside from rats, another potential stressor to wildlife populations on islands is the pressure of tourist visitation. The effect of nature-based tourism and recreation on global bird populations has drawn relatively little attention in either public or academic forums (Steven *et al.* 2011; Steven & Castley 2013). Of the 35 recognized global biodiversity hotspots (Myers *et al.* 2000), Polynesia-Micronesia supports the most bird species threatened by tourism (Steven & Castley 2013; Bellard *et al.* 2014b). Steven and Castley (2013) determined that 63 birds listed as Critically Endangered and Endangered by the IUCN (2016) are directly threatened by tourism, and that species occurring in coastal areas are amongst those most at risk. Palau is one of the world's top SCUBA diving destinations (IMF 2016), and the majority of this activity occurs in and around the RISL. Many of the beaches and coastal areas on which Endangered megapodes breed are also highly attractive as picnic sites where dive operators bring tourists in large numbers on a daily basis. As a response, the local government has built and maintains facilities on these beaches to support and cater to these activities.

In addition to tourist activities and facilities potentially having a direct effect on megapode breeding in the RISL, they may also have an indirect impact by augmenting rodent populations through supplementary food provision (Oro *et al.* 2013; Ruffino *et al.* 2013). In the absences of predators, population densities of rats on tropical islands are generally very high because of greater access to relatively rich food resources (Harper & Bunbury 2015). A consistent availability of anthropogenic food resources further enables these populations to endure environmental variability, further increasing their densities and their threat to native fauna (Russell & Ruffino 2012; Ruffino *et al.* 2013). Understanding the potential effects of tourism and rats on Micronesian Megapodes is essential to their conservation in Palau.

Here, I investigate whether rat and tourist presence affect Micronesian Megapode numbers, and whether rat numbers are affected by human presence on islands in the RISL. I undertook active and passive surveys for megapodes and rats on uninhabited islands in the RISL that were classified as either visited or not visited by tourists, and aimed to assess the relationships between rats, megapodes, and tourist presence. I specifically tested the following hypotheses: 1) rat occupancy is significantly higher on tourist visited islands compared to tourist-free islands (Oro *et al.* 2013), 2) megapode relative abundance is significantly lower on tourist visited islands compared to tourist-free islands (Steven *et al.* 2011), and 3) megapode relative abundance is significantly lower on islands with high rat occupancy (Harper & Bunbury 2015). I discuss my findings in the context of future research and conservation management for threatened species on the Rock Islands of Palau.

Methods

Study Area

The Palau archipelago (7° 30' N, 134° 35' E; Figure 5.1) is the westernmost assemblage of islands in Micronesia. It extends 700 km northeast to southwest and is comprised of 12 inhabited islands and over 500 smaller uninhabited islands and islets (Neall & Trewick 2008; Olsen 2009). Approximately 87 percent of the archipelago is forested, 75% of which is classified as native tropical lowland rainforest (Kitalong *et al.* 2013). My research was focused primarily on the uninhabited islands of the RISL that lie between Babeldaob to the north and Peleliu to the southwest (Figure 5.1), where

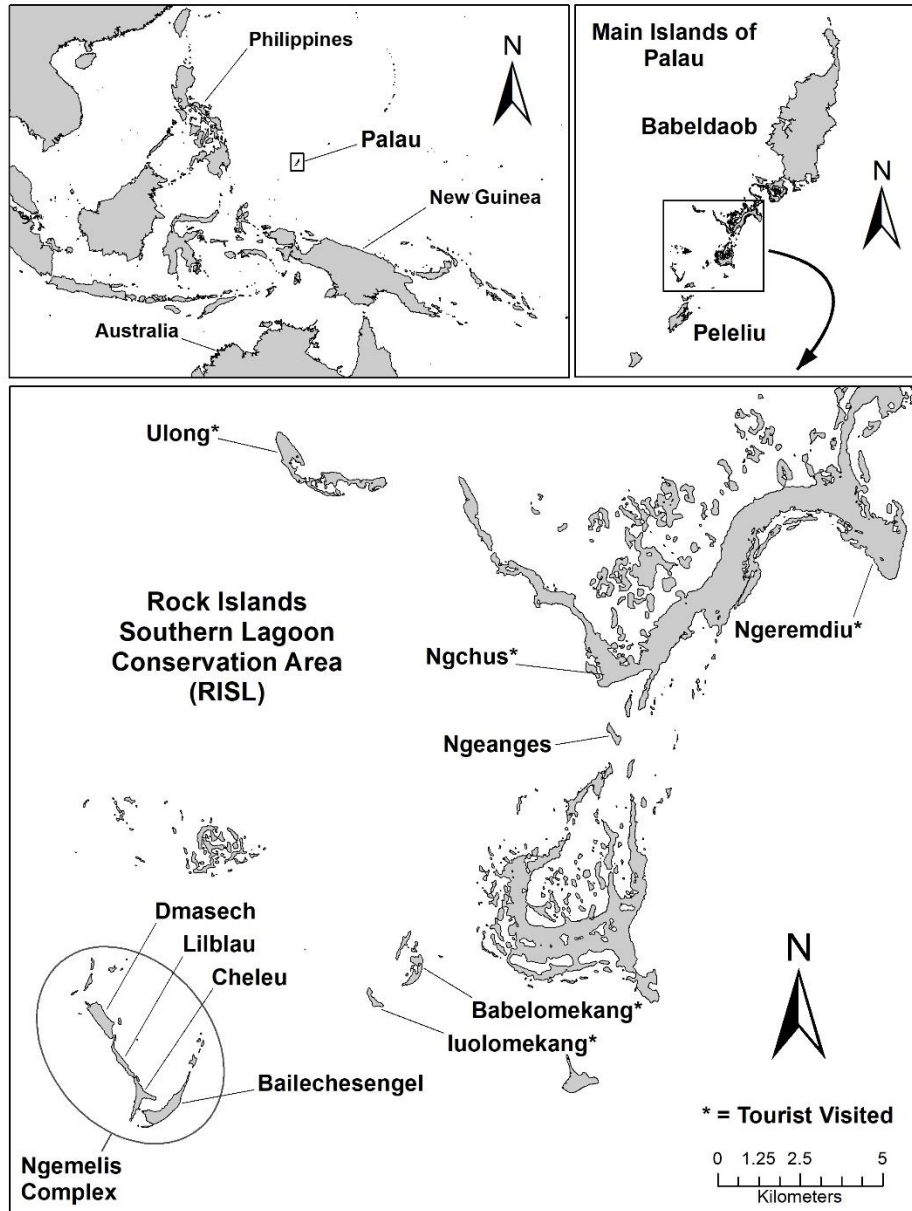


Figure 5. 1. Map of the study area within the Rock Islands Southern Lagoon Conservation Area (RISL), Palau, and the locations of five tourist visited and five tourist-free islands surveyed for rats and megapodes between 15 December 2016 and 22 January 2017.

megapodes are relatively abundant (Olsen *et al.* 2016). Unlike other islands in the archipelago, these “rock islands” are ancient, uplifted reefs and are thus coralline in nature (Engbring 1988). Although some have sandy littoral zones that are heavily visited by tourists, the vast majority of islands in the RISL are characterized by nearly

vertical, highly fissured and eroded, densely forested karst slopes that protrude abruptly from the water, and are undercut at the water's edge (Pratt *et al.*, 1980; Engbring, 1988). Despite the heavy forest cover, these uplifted areas of the RISL exhibit very little soil development and provide no suitable substrate for megapodes to construct their mounds (Pratt *et al.* 1980; Olsen *et al.* 2016).

Survey Island Selection

Islands in the RISL selected for surveys were characterized not only by nearly inaccessible uplifted limestone features, but also by the occurrence of a fringing, sandy littoral zone with the presences of level, beach strand forest cover, which falls under the category of “Limestone Forest” (Kitalong *et al.* 2013). This ecotype was identical in plant species composition and structure at all study sites (Chapter 3). Although rats are known to occur in all terrain of the islands in the RISL (pers. comm., T. Hall), areas of beach strand cover were solely selected for my surveys because of their exclusive use for tourist activities on visited islands, and because they are preferred by megapodes for breeding (Wiles & Conry 2001; Olsen *et al.* 2016), and because of the nearly inaccessible nature of the limestone areas of the islands. Tourist visited islands were additionally characterized by the presence of picnic tables and barbeque facilities, roofed shelters of varying sizes, and restrooms situated in cleared and maintained areas just off the beach. I specifically selected islands for surveys based on 1) the existence of a large enough area of littoral strand forest zone capable of accommodating full length (180 m) rat survey transects, and 2) the level or degree of human visitation they received (Figure 5.1). Of six islands in the RISL that are regularly visited by tourists throughout the year, the five I chose for surveys both met the above size criteria and received moderate to heavy tourist visitation. Four of the selected tourist-free islands were located in the Ngemelis Complex (Figure 5.1), a local government conservation area from which tourists are prohibited. The fifth, Ngeanges, was known to receive only occasional day visits by locals or kayakers. It should be noted that in this sense, none of the islands in my study were truly unvisited “controls”, but represent a contrast between heavy tourism and very occasional local use.

Rat Presence / Absence Surveys

I quantified rat presence with the use of peanut butter scented WaxTags® (www.traps.co.nz). Transects of 10 waxtags spaced 20 meters apart (for a transect length of 180 m) (Ruffell *et al.* 2015a; Ruffell *et al.* 2015b) were established in the available and accessible strand forest habitat on all islands selected for surveys, where tags were secured to trees approximately 10 cm above the ground. Each transect was run parallel with the shore roughly equidistant between the beach and the limestone face behind. The lengths of accessible beach habitat for transects was small and ranged from 185 m to 680 m ($\bar{x} = 419.5$), a portion of which on tourist visited islands was occupied by the facilities described above. Three beaches on tourist islands were just long enough to accommodate 180 m length transects and tourist facilities were by default included in the sampling area. The facilities on the remaining two tourist islands with longer beaches were likewise included in sampling areas to avoid any possible bias in rat detections.

Rat surveys were conducted in two replicates over four nights each, from 15–18 December 2016 and 19–22 January 2017. Waxtags were deployed for two nights across each island type (i.e., tourist visited and tourist-free) during each survey. Given the size of the RISL and the relatively long travel times between some islands via small motorboat, it was necessary to alternate the days of deployment and retrieval of tags by island type. Specifically, tags were deployed and retrieved on days one and three (respectively) of each replicate on tourist visited islands, and deployed and retrieved on days two and four of each replicate on tourist-free islands.

Megapode Call-playback Surveys

My assistant and I established and surveyed a total of 48 megapode count stations in the RISL, 19 on tourist visited islands and 29 on islands not visited by tourists. We collected data on megapode presence and relative abundance on six mornings between 9 and 16 January 2017. Megapode surveys consisted of a combination of stationary call playback counts and spot-mapping conducted on the same beaches and in the same habitat as rat surveys. Count stations were established during counts and were spaced 100 m apart in littoral beach strand habitat approximately 10 m inland from the mean high tide mark. My assistant and I conducted surveys by walking from one end of

target beaches to the other, stopping every 100 m to broadcast pre-recorded megapode calls after acquiring a GPS location of each station. Recordings used for surveys were those of Micronesian Megapodes that I collected in the Rock Islands in February and March 2016. Call playback was projected towards the limestone face behind the beach as megapodes have been observed to not only occur in the littoral strand forest, but also in the dense forest on the face and top of the limestone relief. Surveys at stations consisted of approximately 1-minute of call playback followed by 4-minutes of quiet listening and observation, during which time all megapodes seen or heard were recorded and their general locations relative to the observer mapped in field note books. After completion of each 5-minute playback survey period, we slowly walked to the next station, spot mapping all megapodes seen and/or heard while in transit between stations to avoid double counting birds at successive stations. Birds mapped in this manner were included in count totals at the stations they were detected closest to if it was determined that they had not already been included in station based counts.

Statistical Analysis

I assessed waxtags for evidence of rat chewing for both survey replicates across all islands, recording a '1' for tags that were bitten and '0' for tags that were not. I did not attempt to identify rat species. Site occupancy and detection probabilities for rats were estimated with and without the covariates "Tourist" and "Island" by fitting models in the "unmarked" package in R (Fiske & Chandler 2011). The resulting logit parameter estimates were back-transformed, and model fit and selection were assessed using Akaike's Information Criterion (AIC). To further confirm model fit I compared my occupancy model with a null model of my data using a Likelihood Ratio Test (LRT). Occupancy and detection probabilities were then predicted for rats on tourist visited and tourist-free islands as groups and occupancy was further predicted at the island level; 95% confidence intervals (CI) were generated for all relevant values. Lastly, averaging the number of waxtags bitten across replicates, I used "Tourist" as a covariate to further test for an effect of tourist presence on rat numbers across islands with a Gaussian family generalized linear model (GLM).

To account for small sample sizes and low numbers of repeat samples, I compared my rat occupancy results to those of a Bayesian GLM that provided posterior

means and credible intervals for rat occupancy probabilities for treatment and control island groups, as well as at the island level. To represent a lack of knowledge of the true values of these parameters, the prior probability distribution of both the detection and island occupancy probabilities were assumed to be uniform for this inference. Highest posterior density (HDP) 95% credible intervals were generated for the posterior means of the island level inference while 95% equal-tailed credible intervals were produced for the island group inference (Bolstad 2004).

I was able only to complete one round of megapode call playback surveys (refer to Appendix A), and because of this I could neither calculate detection probability nor estimate site occupancy for the species (Knappe & Korner-Nievergelt 2015). In lieu of occupancy modelling, I first used a Fisher's F-test to evaluate megapode survey sample variance between tourist visited and tourist-free islands to verify homoscedasticity and then compared sample means of the two groups with a two sample t-test. I then employed both a Poisson family GLM to examine megapode detections or abundance at the station level and a logistic regression (Bates *et al.* 2015) to examine megapode presence or absence at the station level. In both models I assessed the effect of tourist presence on megapodes across islands by using "Tourist" as a covariate and "Island" as a random effect, with survey station serving as the observational unit. I employed the Poisson model with the knowledge that the modelled results were not the expected detections or relative abundances of birds, but instead the expected product based on detections and relative abundances across each island type. I applied a Hosmer Lemeshow goodness of fit (GOF) test (Lele *et al.* 2016) to statistically confirm if there was any difference between this model and my observed data and to ensure that the model was correctly specified (Hosmer & Lemeshow 2000).

To test for an effect of rats on megapodes, I first calculated island level relative abundances of the latter and compared them to the Bayesian posterior means of island level rat occupancy probability in a Pearson's product-moment correlation. I followed this with a Gaussian family GLM to model island level megapode relative abundance against rat posterior means and tourist presence, using "Rat" and "Tourist" as covariates. All statistical analysis was performed in program R (R Core Team 2015).

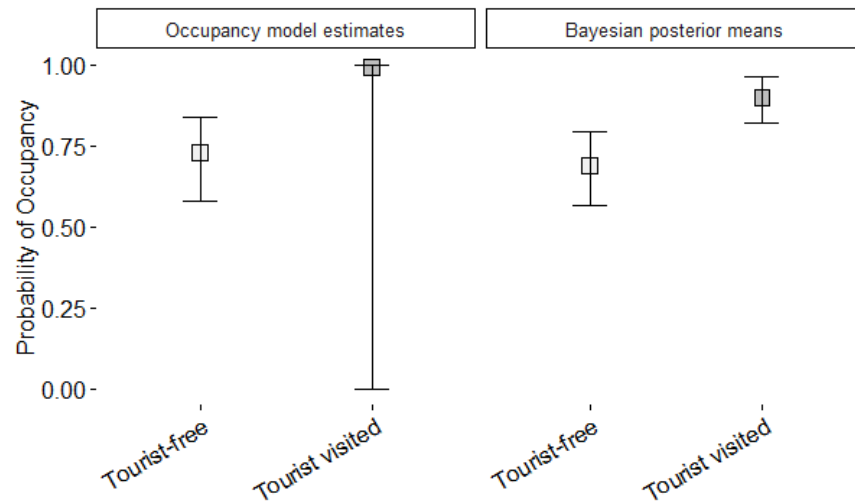


Figure 5. 2. Rat occupancy estimates and 95% confidence intervals compared to occupancy probability Bayesian posterior means and 95% credible intervals for tourist-free and tourist visited islands in the Rock Islands Southern Lagoon Conservation Area (RISL) of Palau.

Results

Rats were detected on all islands surveyed in the RISL, where they chewed a mean \pm SD of 44.5 ± 4.9 waxtags on tourist visited islands and 25.5 ± 9.2 on islands not visited by tourists. Occupancy modelling indicated that the tourist covariate had a significant positive influence on both rat detection probability ($P < 0.001$) and site occupancy ($P < 0.01$). The probability of detecting rats on the tourist visited islands as a whole (0.89; 95% CI 0.80–0.94) was significantly higher ($P = 0.031$) than on tourist-free islands (0.52; 95% CI 0.42–0.62). Likewise, occupancy on tourist visited islands (0.99) was significantly ($P = 0.028$) higher than on tourist-free islands (0.73) and the Bayesian posterior means for occupancy probability (0.90 and 0.69, respectively) were also significantly different ($P = 0.028$) (Figure 5.2). At the island level, occupancy estimates for tourist visited islands ranged from 0.93 to 1.00 and from 0.52 to 1.00 for tourist-free islands while Bayesian posterior means ranged from 0.8553 to 0.9167 and from 0.5192 to 0.9167, respectively (Table 5.1). In all instances, the Bayesian GLM provided equal-tail and HPD credible intervals that were slightly more informative when compared to the occupancy generated CI for each island group and each individual island (Figure 5.2 and Table 5.1). The results of my Gaussian GLM comparing station-level averages of

Table 5. 1. Island level rat occupancy estimates and 95% confidence intervals compared to island level occupancy probability Bayesian posterior means and 95% credible intervals for tourist visited and tourist-free islands in the Rock Islands Southern Lagoon Conservation Area (RISL) of Palau.

Island	Occupancy		Confidence Intervals		Posterior		HPD Credible Intervals	
	Estimate	SE	Lower 95%	Upper 95%	Mean	SD	Lower 95%	Upper 95%
<i>Tourist Visited</i>								
Babelmokang	1.00	0.00041	0.0000	1.0000	0.9167	0.0767	0.7616	1.0000
Ngehus	0.93	0.09883	0.3937	1.0000	0.8553	0.1038	0.6548	1.0000
Ngeremdiu	1.00	0.00003	0.0000	1.0000	0.9167	0.0767	0.7616	1.0000
Ulong	1.00	0.00003	0.0000	1.0000	0.9167	0.0767	0.7616	1.0000
Ioulomokang	1.00	0.00003	0.0000	1.0000	0.9167	0.0767	0.7616	1.0000
<i>Tourist-Free</i>								
Bailechesengel	0.52	0.16378	0.2287	0.7951	0.5192	0.1442	0.2424	0.7961
Cheleu	0.72	0.15026	0.3755	0.9201	0.6921	0.1358	0.4278	0.9418
Dmasech	0.72	0.15026	0.3755	0.9201	0.6921	0.1358	0.4278	0.9418
Litblau	0.62	0.16053	0.3009	0.8619	0.6058	0.1422	0.3299	0.8743
Ngeanges	1.00	0.00002	0.0000	1.0000	0.9167	0.0767	0.7616	1.0000

rat detections across tourist visited and tourist-free islands further supports the hypothesis that tourist presence has a significant positive relationship with rat detections (Table 5.2, model 1).

I recorded 107 megapodes detections during surveys across all 10 islands, yielding a mean detection rate of 10.7 birds per island (range = 1 – 20) (Table 5.3). On tourist visited islands, 30 individual detections were recorded from nine of 19 (47%) count stations compared to 77 detections recorded from 27 of 29 (93%) stations on tourist-free islands. Sample variance between the two island groups was confirmed to be homoscedastic ($P = 0.221$). Relative abundance (i.e., mean birds per station or BPS) of megapodes on tourist islands (1.58 BPS, $SD \pm 2.29$) was significantly different ($P = 0.013$; Mann-Whitney non-parametric test) from that on tourist-free islands (2.66 BPS, $SD \pm 1.78$), and presence of megapodes at survey stations was significantly lower ($P = 0.026$; logistic regression [Table 5.2, model 2]) on tourist islands. The results of the Poisson GLM indicated that although the tourist covariate appears to have a slight negative influence on megapode relative abundance, the coefficient was not significantly different from the intercept (Table 5.2 model 3). The Hosmer Lemeshow GOF test was non-significant ($P = 0.51$) when comparing the Poisson model and my observed data, thus confirming that the model was a good fit.

A Pearson's product-moment correlation conducted at the island level showed a weak but non-significant negative relationship (-0.49 , 95% CI -0.85 – 0.20 ; $P = 0.152$) between rat occupancy and megapode relative abundance. The results of the Gaussian GLM indicated that while both the covariates rats and tourists appeared to have a slight negative influence on megapode relative abundance, the coefficients were not significantly different from the intercept (Table 5.2, model 4).

Discussion

My results suggest that tourist presence may both negatively affect overall megapode abundance in the RISL, and decrease megapode detection rates at the stations I surveyed. My results do not strongly indicate, however, that megapode relative abundance is negatively affected by tourist presence at the island level. This result may be owed to the fact that two islands, Babelmokang and Ulong, yielded relatively high station level relative abundances (i.e., BPS) and detection rates of 100% (Table 5.3)

Table 5. 2. Results for four models used to assess the effect of tourist presences on rats (model 1) and Micronesian Megapodes (model 2 and 3), and the effect of rats on scrubfowl (model 4) on tourist visited and tourist-free islands in the Rock Islands Southern Lagoon Conservation Area (RISL) of Palau.

Parameter	Estimate	SE	t/z-value	Pr (>t/z)
<i>Model 1, Gaussian GLM – Rats on tourist visited vs tourist-free islands</i>				
Intercept	0.5100	0.0464	11.004	0.0000
Tourist Visited	0.3700	0.0655	5.645	0.0000
<i>Model 2, Logistic Regression – Megapode presence / absence at survey station level on tourist visited vs tourist-free islands</i>				
Intercept	3.064	1.067	2.871	0.0041
Tourist Visited	−2.798	1.259	−2.223	0.0262
<i>Model 3, Poisson GLM – Megapode relative abundance at survey station level on tourist visited vs tourist-free islands</i>				
Intercept	0.9559	0.2744	3.484	0.0005
Tourist Visited	−0.7276	0.4341	−1.676	0.0937
<i>Model 4, Gaussian GLM – Effect of rats on Megapodes across islands</i>				
Intercept	5.766	3.414	1.689	0.142
Rats	−4.285	4.893	−0.876	0.415
Tourist Visited	−21.777	24.093	−0.904	0.401
Rat: Tourist Visited	23.788	26.810	0.887	0.409

despite receiving high levels of tourist visitation (pers. obs., P. Radley). In this context, these two islands stand in stark contrast to the remaining three tourist visited islands in the RISL, both of which yielded exceedingly low station level relative abundances and detection rates when compared with islands that were off limits to tourists (Table 5.3).

Previous studies have highlighted the negative consequences of tourism and recreation based activities on avian densities and abundance (e.g., Steven *et al.* 2011). Aside from negative consequences to individual physiology and reproductive success, other studies (e.g., Otley 2005; Ma & Cheng 2008; Steven *et al.* 2011; Steven & Castley 2013) show that the behaviour, distribution and movement patterns of some bird species in tourist visited areas are affected by human presence, while their apparent abundance or numbers are not. Otley (2005) further found that up to 80% of Gentoo *Pygoscelis*

Table 5. 3. Total counts and relative abundances during call playback surveys for Micronesian Megapode on tourist visited and tourist-free islands in the Rock Islands Southern Lagoon Conservation Area (RISL) of Palau. No. of Stations is the number of survey stations per island, Count Total is the total number of megapodes counted per island, BPS is the mean number of birds detected per station, and % Stations w/ Detections is the percentage of stations per island at which megapodes were detected.

Island	No. Stations	Count Total	BPS	% Stations w/ Detections
<i>Tourist Visited</i>				
Babelmokang	2	5	2.50	100%
Ngchus	3	2	0.67	33%
Ngeremdiu	6	1	0.17	17%
Ulong	5	19	3.80	100%
Ioulomokang	3	3	1.00	33%
<i>Not Tourist Visited</i>				
Bailechesengel	4	20	5.00	100%
Cheleu	6	14	2.33	100%
Dmasech	7	19	2.71	100%
Lilblau	7	12	1.71	86%
Ngeanges	5	12	2.40	80%

papua, King *Aptenodytes patagonicus*, and Magellanic *Spheniscus magellanicus* Penguins at a tourist visited sites in the Falkland Islands avoided traveling between beach and colony areas during daylight hours when most human visitors were present. Indeed, megapodes on tourist visited islands in the RISL tended to be more skittish upon approach than on islands that experience little or no human presence (pers. obs., P. Radley). From a statistical standpoint, however, my Poisson GLM indicates a slight negative effect of tourism on megapode relative abundance. The relatively high number of birds detected on Babelmokang and Ulong (Table 5.3) may have prevented this model from showing a significant result. This may leave the result of my logistic regression to be a more accurate reflection of the effect of tourists on megapodes.

My results also show that tourist presence may positively influence rat numbers. The probability of detecting rats on islands that routinely receive high levels of tourist visitation was 42% greater than on islands that were tourist-free. While occupancy on tourist-free islands was relatively high and the difference between these islands and

tourist-visited islands is lower than the difference between detection probabilities, occupancy on tourist islands approached 1.00. I cannot rule out that these differences are not the result of historical visits by local people for the purpose of fishing or hunting coconut crabs (*Birgus latro*). One likely reason for this disparity, however, is that high tourist presences often equates to the greater availability of food waste that may supplement the diet of rats on islands routinely and heavily visited by tourists (e.g., Sealey & Smith 2014). Although the level of tourist presence visiting islands may vary throughout the year, tourists are present in the RISL year-round (pers. comm., Koror State Government). Depending on the season, an island's infrastructure, and its proximity to popular dive sites in and around the RISL, several dozens to near a hundred tourists could be fed buffet style at the picnic facilities on a single beach every day (pers. obs., P. Radley). The resulting waste was often left at these facilities in plastic bags for the local government clean-up crews to remove for disposal. In some instances, smaller portions of organic waste were simply discarded by locals, tourist and tour operators in the vegetation adjacent to picnic facilities.

There are numerous published studies illustrating the effect of tourism, particularly nature-based tourism, on wildlife populations (e.g., Steven *et al.* 2011; Steven & Castley 2013). Surprisingly, however, I could find little pertaining to the possible direct effects of tourism activities on populations of invasive rats, particularly in tropical island ecosystems. Only Sealey and Smith (2014) describe high concentrations of rats at tourist facilities as a result of the availability of solid food waste generated by tourist based operations on Great Exuma Island, Bahamas. That study, however, focused specifically on large facilities or resorts on the island, and sheds no light on its broader ecological effects on rats at the ecosystem level (Sealey & Smith 2014). Resource subsidies across numerous ecosystems, however, have been found to increase individual fitness and resilience of various opportunistic species, leading to increases in densities and decreases in temporal variability of some populations (Oro *et al.* 2013). Insular rodents with access to allochthonous resources tend to grow larger, occur at higher densities, and their populations tend to persist in the longer-term in part because they are better able to withstand local environmental stress (Stapp & Polis 2003; Ruffino *et al.* 2013). My field observations strongly indicate that food subsidies are routinely made available to rats on islands in the RISL, and that this

is likely to present a significant challenge to rat-sensitive species inhabiting these islands.

My results further suggest that the presence of rats may not significantly affect or suppress megapode presence on islands in the RISL. Numerous other studies that have attributed island bird extinction and extirpation to the presence of invasive rats (e.g., Tabak *et al.* 2014; Harper & Bunbury 2015). The outcome of my results, however, may reflect the differences between the natural history traits megapodes and other species of island birds. Rats (particularly black rats) affect island landbird populations primarily at the level of productivity by depredating eggs, hatchlings or chicks in nests, but they also opportunistically take adults of some smaller species (Shiels *et al.* 2013; Harper & Bunbury 2015). Unlike other avian species, megapode eggs and hatchlings are not outwardly visible and vulnerable to predation for days to weeks on end within an open nest. Instead, their eggs are buried under up to a meter of sand or soil and organic matter, through which hatchlings dig their way to the surface after hatching (Jones *et al.* 1995). A young megapode would be most vulnerable for a relatively brief period just as it erupts from the incubation mound, after which it emerges as a “super-precocial” chick that cannot only run but is immediately capable of flight (pers. comm., R.W.R J. Dekker). The window of opportunity for predation by rats is therefore relatively very narrow and any megapode young taken by rats may likely be more so by chance. The lack of an obvious or significant effect in my study may be due to the fact that rat predation is negligible on larger sub-adult and adult birds.

Some studies show that other island birds are able to coexist with introduced rats with no apparent negative effects at the population level. Larger, ground nesting seabirds (e.g., albatrosses, frigatebirds, and gulls) tend to be far less affected by rats than smaller, burrow nesting seabirds (e.g., storm petrels and some Alcids), a result that may stem from the size of the former and their likely adeptness at defending their eggs and young from predators (Jones *et al.* 2008). Populations of larger burrow nesting shearwaters that breed almost exclusively on rat infested islands in the Mediterranean were found to be limited less by rats than the smaller, resident storm petrels, and more so by physical characteristics of the islands themselves (Ruffino *et al.* 2009). Tabak *et al.* (2014) found that the occurrence of three mostly ground-dwelling passerines, the Falkland Pipit *Anthus correndera*, Long-tailed Meadowlark *Sturnella loyca*, and Dark-faced Ground Tyrant *Muscisaxicola maclovianus*, were unaffected by the presence of

Norway rats *R. norvegicus* in the Falkland Islands, regardless of island size. While the endemic pipit avoids areas of tussock grass *Parodiocloa flabellata*, a habitat preferred by Norway rats, the above-ground feeding behaviours of the latter two may reduce their exposure to rats (Hall *et al.* 2002). Hall *et al.* (2002) additionally hypothesized that former exposure to the now extinct Falkland Islands wolf *Dusicyon australis* may have aided to maintain ancestral inherited anti-predator behaviour in populations of some species.

There is the possibility that rats serve as a competitor for food resources (Shiels *et al.* 2013), but my data are not appropriate to test this hypothesis. Although there is little in the literature pointing to rats as direct resource competitors for avian species (Shapiro 2005; Tabak *et al.* 2016), Shiels *et al.* (2013) suggest that those birds relying on either arthropods or fruit as a major component of their diet may experience direct competition with rats. The Micronesian Megapode is omnivorous, with a diet consisting of a variety of fruits, seeds and other plant matter, various insects and land crabs (Jones *et al.* 1995). Likewise, both species of rat that occur in the RISL are known to be highly opportunistic, exploiting virtually any available food source, but relying heavily on plant matter, with insects providing the majority of animal protein in their diets (Shiels *et al.* 2013; Harper & Bunbury 2015). The broad dietary intake of megapodes in the RISL may serve to minimize the chances of direct resource competition, and as primarily a scratch feeder the species may fill a functionally different foraging niche than rats (Jones *et al.* 1995).

Habitat and Megapode Detectability

While Palau supports the richest assemblage of native flora and the highest rate of plant endemism in Micronesia (Costion *et al.* 2009), plant diversity across islands in the RISL is relatively homogenous (Chapter 2; Kitalong 2014). Based on this, and on the fact that the RISL supports the majority of breeding megapodes in the archipelago, with incubation mounds occurring on all islands surveyed, I assumed that habitat would not be a factor in my analysis of megapode relative abundance.

The only comprehensive survey of megapodes in the Palau archipelago was conducted by Olsen *et al.* (2016), in which a combination of 15-minute passive counts and broad area searches (for birds and mounds) were used to survey 122 beach / island

sites. They detected 350 individuals at 61 (50%) of the sites surveyed, for a detection rate of 2.9 megapodes per beach or island included in the surveys. Olsen *et al.* (2016) suggested one confounding factor that could have decreased their detections is the possibility of “commuting” by megapodes between their nesting and feeding grounds, a phenomena documented in other species (pers. comm., R.W.R.J. Dekker; Jones *et al.* 1995). As a result, birds may have at times been detected on return visits at sites where they had not previously been encountered, or not detected at sites they previously had (Olsen *et al.* 2016).

By comparison, my surveys yielded a mean detection rate of 10.7 megapodes with at least one bird detected at every one of the 10 beaches or islands surveyed in the RISL. This difference may likely have been the result of my use of a targeted active survey, employing call-playback from fixed stations at survey sites. Many of the detections made by my field assistant and I were of birds that responded from a distance from habitat atop the limestone relief, birds we would not have detected without call-playback. Given my relatively high detection rates, and the fact that we detected birds at every site surveyed, commuting by megapodes may not have been encountered on the islands we surveyed during my work.

Conservation Implications

In March 2017, Island Conservation executed an eradication of rats from the island of Ngeanges and was developing plans with the local government to do likewise for other islands in the RISL (pers. comm., T. Hall). This is inarguably the optimal approach to conservation of tropical island landbird species threatened by rats (e.g., Russell & Holmes 2015; Jones *et al.* 2016; Spatz *et al.* 2017). While my results suggest that rats do not detrimentally affect megapodes, other species of native and endemic landbirds that share forested habitat with megapodes in the RISL are at threat (e.g., Harper & Bunbury 2015). Aside from some point-count based inventories (e.g., VanderWerf 2007), few studies have been carried out on Palau’s terrestrial avifauna and little is known about population trends for most species in the RISL. Given the significantly higher level of rat detection probability and occupancy on tourist visited islands relative to tourist-free islands, a study comparing the vital rates of landbirds across the two island types would be beneficial (e.g., Saracco *et al.* 2014). The threat of rats to island

landbirds suggests that quantitative studies concerning the effect of tourism on rat populations would be an asset to other insular nature-based tourism destinations globally.

To further manage rat numbers in the RISL, a good first step would be managing tourist waste by enforcing a “pack-it-out” policy that requires tourist operations to remove all their food waste from the islands they visit. Adequate signage, education and onsite enforcement of removal of all food refuse by tourist operators would go a long way to decrease supplementary food sources that may be helping to sustain or augment rat populations on tourist visited islands in the RISL.

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CHAPTER 6: Synthesis and Conclusion

In the preceding chapters of this thesis, I opened by examining the effect of climate change on the avian family Megapodiidae. I then narrowed the scope of my investigation to define breeding and foraging habitat for the Micronesian Megapode in the Rock Island Southern Lagoon Conservation Area (RISL) of Palau. Following this, I assessed the effect of predicted sea level rise on their breeding habitat, which is important not only to the life history of the Micronesian Megapode, but to its long term survival in the Palau archipelago. I ended by investigating the effect of introduced rats and tourist pressure on megapodes in the RISL, and examined the potential impacts of each on this species of island bird that is threatened by rising sea levels resulting from climate change.

Here, I begin by summarizing the primary findings of my research as described in this thesis, in relation to my original research objectives for this work. Following this I provide a synthesis of my results from the perspective of the Micronesian Megapode as a species, and discuss how my findings relate and are transferrable to the remainder of the population in Palau outside of the RISL. I then compare IUCN (2016) listed threats to the Micronesian Megapode by subspecies, and propose 1) a new threat ranking for each subspecies based on version 3.2 of the IUCN Threat Classification Scheme, and 2) an additional climate change related threat for the species based on the results of my sea level rise modelling for the RISL. I end by proposing suggested research and data necessary to fill gaps in our knowledge of megapode ecology in Palau and to understand the conservation needs of the subspecies.

Summary of Major Findings

Objective 1. *Quantitatively assess the threats of climate change to the megapodes based on their biological or ecological traits that may be most affected.*

Unlike any other family of birds, the one trait that may cause megapodes to be uniquely vulnerable to climate change is their evolutionary strategy of relying solely on environmental (i.e., external) sources of heat to incubate their eggs. To quantify the level of threat to the family Megapodiidae, I employed a trait-based vulnerability

assessment (TVA) to determine the susceptibility of 21 species to increasing temperatures, fluctuations in rainfall, and sea level rise across their individual ranges. While all species will be affected by some aspects of climate change, I determined that the species that were most susceptible and ranked most vulnerable to climate change are relatively rare habitat specialists that are confined to highly restricted ranges, specifically islands. The most vulnerable species also tended to be moderately to highly isolated with little avenue of retreat (if necessary) from their limited ranges, aside from long distance over water flight.

While intrinsic sensitivity was the deciding factor in the vulnerability of seven species, extrinsic exposure was the most important for the remainder, although not by a large margin. All but one species of megapode will be subjected to a relatively high increase in temperatures. Fifteen species will be exposed to an increase in mean annual rainfall, which may have little adverse effect on them given that most employ microbial decomposition of organic matter as a heat source for incubation. Considering the unique homeothermic qualities of incubation mounds (Sinclair 2001) and the resilience of megapode embryos to fluctuating incubation temperatures (Eiby & Booth 2008), species that rely on microbial decomposition may be at a greater adaptive advantage than those that do not in the context of increasing temperatures and changes in rainfall. An overall increase in warmth and moisture could even benefit these species by increasing the availability of forest biomass, and thus the organic matter essential to mound incubation.

Seven of the 15 species predicted to be exposed to increased precipitation will further experience an increased seasonality in rainfall, characterized by longer and more intense dry seasons. Mound incubating species may be able to weather this climatic change by perhaps shifting their breeding seasons and laying dates as necessary. However, the potential benefits conferred by an overall increase in moisture for mound incubation may be diminished by the synergy between a seasonally dryer climate and contemporary human forestry practices throughout this region. The cumulative range of more than half of the world's megapode species (Indonesia, the Philippines, and Timor-Leste) experiences some of the highest known rates of deforestation, and the use of fire for land clearing is ubiquitous throughout this region. Warmer and seasonally drier conditions, coupled with common place human-ignited wildfires, may exacerbate loss of habitat and biomass, and the stable microclimate necessary for mound incubation.

Sixteen species of megapode will be exposed to rising sea levels, eight of which will be at least moderately affected by it. My TVA ranked only two species, the Moluccan and Nicobar Megapodes as highly vulnerable to inundation given the close proximity of their breeding areas to the ocean and its fluctuating tides.

Objective 2. *Define the nesting and foraging habitat used by the Micronesian Megapode in the RISL of Palau.*

To identify the habitat specific variables megapodes in the RISL may select for when choosing incubation and foraging sites, I collected habitat and environmental data at both mounds and foraging sites and compared these to the same data collected at randomly chosen sites. I found that habitat variables were statistically different from random at only mound base areas (i.e., at mounds themselves). Neither variables within the forest immediately surrounding mounds, nor those at foraging sites, were assessed to be significant. More specifically, I determined that megapodes in the RISL non-randomly selected incubation sites that were relatively close to shore, contained very large trees (> 70 cm DBH), and exhibited greater canopy heights than the surrounding forest. These findings are similar to those for other species of megapodes in New Guinea, Indonesia, and northern Australia (e.g., Jones 1988; Sinclair 2002). The presence of large trees and high canopy at incubation sites in the RISL is owed to the fact that 83% of mounds were constructed at the bases of trees, the majority of which were well over 100 cm DBH. Forty-five percent of these mounds were built at the bases of ironwood trees, a salt tolerant species native to the Western Pacific that is ubiquitous to sandy coastal areas and a common component of littoral strand habitat.

Other species of megapodes in the Indo-Pacific and Australasia were additionally found to non-randomly select sites with significantly denser canopy cover (e.g., Sinclair 2002). A thick, dense canopy is necessary to support the relatively moist and thermally stable sub-canopy microclimate necessary for mound incubation. My findings suggest that forest canopy of the low lying littoral habitat within the RISL is consistently closed, with cover densities approaching 100% throughout. Megapodes in my study site, therefore, do not need to select incubation sites based on this habitat variable.

I also collected data to determine if there was dominance in seedling, sapling, and / or mature tree species at mound and foraging sites compared to random. I found that site specific dominance was only significantly different between mound base areas and random and only for trees. While breadfruit was more likely to be dominant at base areas, and coconut and Java-apple more likely dominant at random sites, nearly half of base areas contained no dominant species compared to 11% of random sites. This difference was the driving factor in the overall difference in dominant tree species between mound base areas and random sites, with base areas much less likely to exhibit a clear dominant and support more of a mix of tree species compared to the surrounding forest.

Objective 3. Investigate the effect of projected sea level rise on megapode foraging and breeding habitat in the RISL and identify possible refugia within the archipelago.

To assess the effect of sea level rise on megapodes in the RISL, I acquired GPS locations of 198 incubation mounds in the conservation area. I delineated and plotted as polygons all forested habitat in the RISL in ArcMap (ESRI 2015) and then used the mound locations to further delineate, plot and quantify current megapode breeding habitat. Lastly I used ArcMap to search for, delineated and quantified all potential breeding habitat. I then modelled the effect of three scenarios of RCP 8.5 sea level rise, 0.52 m, 0.98 m, and 1.9 m (Church *et al.* 2013; Jevrejeva *et al.* 2014), on all known and potential megapode breeding habitat in the RISL.

Megapodes use 3.1% (120.8 ha) of the 3,857.5 ha of forested habitat in the RISL for breeding. Separate areas of known breeding habitat ($n = 38$) ranged from 0.07 ha to 41.9 ha in size, while 72 areas of potential breeding habitat totalled 25.3 ha and ranged in size from 0.02 ha to 3.8 ha in area. Under the three modelled scenarios of predicted sea level rise (0.52 m, 0.98 m, and 1.9 m, respectively) 32.5%, 36.4%, and 43.3% of total known and 25.7%, 27.6%, and 31.3% of total potential megapode breeding habitat may be lost in the RISL to inundation. Considering known and potential breeding habitat together (146.1 ha), under the worst-case scenario for which I modelled (1.9 m of eustatic rise), at most only 2.2% of all forested cover in the RISL would be available to and suitable for megapode breeding.

Objective 4. *Determine the effect that introduced rats and tourists have on megapodes in the RISL as added stressors to sea level rise.*

Using passive chew tag surveys for rats and dynamic call playback surveys for megapodes, I examined rat occupancy and megapode relative abundance across five tourist visited and five tourist-free islands in the RISL. Contrary to the findings of numerous other studies pertaining to the effect of rats on island birds (e.g., Tabak *et al.* 2014; Harper & Bunbury 2015), my results suggest that rats do not directly or negatively impact megapodes in the RISL. My findings further suggest that although tourist presence may have no effect on megapode relative abundance, this presence might affect the distribution of megapodes on islands that tourists routinely visit. This points to a behavioural response to human visitation to islands they use for rest stops during diving and for picnics.

Objective 5. *Examine the role that tourist presence plays in maintaining and augmenting rat populations in the RISL.*

Analyses to meet the goals of Objective 4 suggest that tourist presence does maintain and positively affects rat populations in the RISL. Both rat occupancy and detectability were significantly greater on islands that were tourist visited, the former approaching 1.00, the latter 42% greater on islands in the World Heritage site that receive heavy tourist visitation. Personal observation suggests that the sometimes copious presence of allochthonous resources in the form of human food waste was, not surprisingly, likely directly responsible for these differences between visited and non-visited islands.

Synthesis

Throughout my thesis I have evaluated and examined the effect of climate change on megapodes, with particular attention paid to the subspecies of Micronesian Megapode that occurs in the island nation of Palau. As discussed in previous chapters, the species consists of two subspecies, the nominate *Megapodius laperouse laperous* occurring in the Mariana Islands and *M. l. senex* in Palau. Although there are some morphological and vocal differences between these two populations, and some researchers indeed

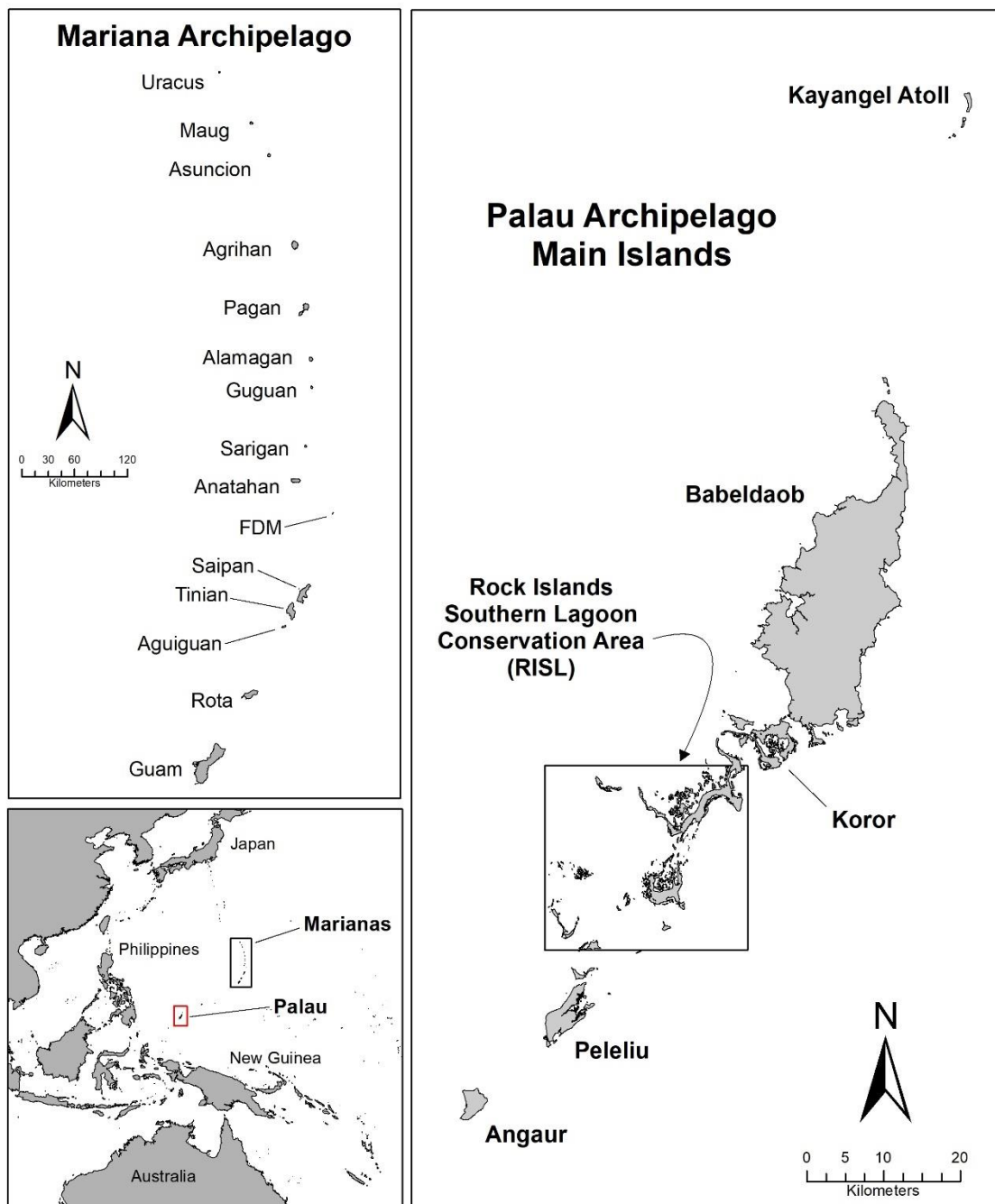


Figure 6. 1. Range of the Micronesian Megapode (*Megapodius laperouse*). In the Mariana Archipelago, FDM is short for ‘Farallon de Medinilla’. The nominate subspecies, *M. l. laperouse*, occurs in the Mariana Archipelago, while *M. l. senex* occurs in Palau.

suggest they are very likely separate species (pers. comm., D. Pratt; Pratt 2010), for the purpose of discussion here I continue to consider them as belonging to one species. Although *M. l. laperouse* once inhabited all islands in the Mariana Archipelago (Figure 6.1) (Steadman 2006), the population is now primarily confined to the relatively young, volcanic islands north of FDM, with the exception of a small population occurring on this island, Saipan and Aguiguan, and occasional records of one or two individuals from Tinian (Wiles 1987; USFWS 1998; O'Daniel & Krueger 1999; Amidon *et al.* 2011). While the records for Tinian may have been the result of birds commuting or dispersing from either nearby Aguiguan or Saipan (Wiles 1987; O'Daniel & Krueger 1999), evidence suggests that the small population on Saipan was the result of the local human populace more recently reintroducing the species from islands to the north after they had been extirpated from the island in the 1930's (Glass & Aldan 1988).

In the Marianas (Figure 6.1) the megapode primarily occurs in native forest (volcanic forests to the north of FDM, limestone forests on this island and to the south), but on the islands north of FDM it will occur equally in stands of coconut forest; on the islands of Asuncion and Sarigan, for instance, there was no significant difference between the abundance of megapodes found in these two forest types (Amidon *et al.* 2011). Glass and Aldan (1988) are the only researchers to specifically investigate territoriality, spatial patterns, and habitat use by the Micronesian Megapode, both in the Marianas and for the species as a whole. Research on Saipan (Figure 6.1) led Glass and Aldan (1988) to hypothesize that megapode pairs stayed together throughout each year, using relatively small home ranges that they advertised and defended seasonally. Only 28% of sightings were in secondary forest habitat, the remainder in native limestone forest (Glass & Aldan 1988). Intriguingly, locations estimated by Amidon *et al.* (2011) for megapodes on Saipan in 2010 all fell within the home ranges estimated by Glass and Aldan (1988) in the mid 1980's, an indication of strong site fidelity by the Marianas subspecies. On Guguan (Figure 6.1) birds were regularly observed in most areas and habitat except for extremely barren volcanic slopes and dense swordgrass (*Miscanthus floridulus*) thickets (Glass & Aldan 1988). The majority of megapodes documented in areas of beach morning-glory (*Ipomoea pes-caprae*) and tussock-grass (*Heteropogon contortus*) were thought to be juvenile or sub-adult, and densities were lower than those in forested areas (Glass & Aldan 1988).

Although Micronesian Megapodes in Palau are well documented using littoral strand forest for construction of their incubation mounds (Baker 1951; Wiles & Conry 1990, 2001; Olsen *et al.* 2013), no formal or targeted studies of its habitat use are found in the published literature. My study of breeding habitat pertained specifically to the microhabitat variables that may influence megapodes in the RISL when choosing incubation sites. I thus focused my investigation on extant, active incubation mounds in littoral strand forest. I determined that birds in this habitat cover type preferentially chose incubation sites that were located close to shore, contained large trees and exhibited relatively high forest canopy structure. The significance of the latter two traits at incubation sites, i.e., large trees and high canopy, is not surprising given that 83% of the active mounds for which I measured habitat were built at the base of very large trees. The fact that 70% of the 198 mounds I located during my field work were free standing (i.e., not built at the base of a tree) presents what seems to be an air of bias in my assessment of megapode breeding habitat in the RISL. However, the 24 mounds at which I collected habitat data were simply all the incubation mounds that were active and /or under construction on the seven islands to which my data collection was restricted (Appendix A). Although not quantified, it was readily apparent to me in the field that megapodes chose the largest trees available in the littoral habitat (the majority of them ironwood) on these seven islands for mound construction.

Marshall (1949) had previously noted megapodes to be relatively abundant in the Rock Islands, where he observed them foraging amongst the limestone or karst formations on these islands. This and similar reports documented in Baker (1951) are apparently the only published observations specifically pertaining to foraging by *M. l. senex*. Given the steep and nearly inaccessible nature of limestone specific forests on these islands, I concentrated my data collection for foraging birds in the same littoral habitat they used for incubation. I found that megapodes non-preferentially forage throughout this cover type in the RISL, a lack of selectivity that may be attributable to the species' omnivorous and generalist approach to feeding (Jones *et al.* 1995).

Although megapodes in Palau are only known to incubate their eggs in mounds (Olsen *et al.* 2013; Olsen *et al.* 2016), those in the Marianas have been documented employing all three incubation strategies typical of megapodes (Baker 1951; Ludwig 1979; Glass & Aldan 1988; Stinson 1992). Given the lack of littoral strand forest, megapodes on the islands north of Saipan are known to rely primarily on heat generated

by either passive solar radiation or geothermal activity (Ludwig 1979; Glass & Aldan 1988), the latter of which is facilitated by the moderate level of volcanic activity exhibited by these islands (Bloomer *et al.* 1989). While Ludwig (1979) also describes what could possibly have been an incubation mound built by megapodes well above the beach on the slopes of Agrihan, Stinson (1992) had later discovered a likely mound on the raised karst platform island of Aguiguan. Mound incubation specifically in littoral strand forest has only been documented on Saipan (Baker 1951), the only southern island on which megapodes have bred in recent history that provides this cover type. Although most littoral strand forest on this island has since been replaced either with beachfront residences or large resorts (pers. obs, P. Radley), mounds in this habitat on Saipan were described in Baker (1951) as being very similar in construction to those currently built by *M. l. senex* in the RISL of Palau (Wiles & Conry 2001; Olsen *et al.* 2016). Aside from these records, very few specifics are known about megapode breeding in the Marianas.

The most recent population estimates for megapodes in the Marianas were based on point-transect distance surveys (Buckland *et al.* 2001) conducted in 2010 at 516 stations along 60 transects established across eight islands in the archipelago (Saipan, Sarigan, Guguan, Alamagan, Pagan, Agrihan, Asuncion, and Maug; Figure 6.1) (Amidon *et al.* 2011). The total abundance estimated for these islands was 10,727 individuals (95% CI 6,682 – 15,445) with 73% of this reported for Asuncion and Sarigan (n = 5,714 and 2,135, respectively) (Amidon *et al.* 2011). In 2009, surveys at 74 stations along six transects on Aguiguan (Figure 6.1) yielded an additional estimate of 112 individuals (range = 61 – 206) (Amidon *et al.* 2010). In Palau (Figure 6.1), variable circular plot surveys (or VCP, the precursor to point-distance transect surveys) were conducted in 1991 by Engbring (1992) at 592 stations along 36 transects established throughout the archipelago (excluding Kayangel Atoll), which yielded a total abundance of 497 megapodes. Densities during these surveys were highest on Angaur (12 birds / km²) and lowest on Babeldaob (1 bird / km²), with population estimates of 244 individuals on this latter island, 104 in the Rock Islands, 52 on Peleliu, and 97 on Angaur (Engbring 1992). In 2005, VanderWerf (2007) surveyed these same transects with the inclusion of 25 stations along three additional transects, employing the same VCP methods used by Engbring (1992). These surveys yielded a total of 27 birds detected, and although absolute abundances were never calculated (pers. comm.,

E. VanderWerf), relative abundances (mean number of birds per station) ranged from 0.01 on Babeldaob to 0.26 on Angaur, with the second highest abundance reported as 0.09 in the Rock Islands (VanderWerf 2007). Although transect-specific abundance was highest along the one placed in the Ngerukuid Islands Wildlife Preserve (a locally designated conservation area; Chapter 3), VanderWerf (2007) reported a decline in megapode abundances since 1991 in the Rock Islands, as well as on Angaur. No other archipelago-wide survey for megapodes have been completed in Palau to date.

I chose the RISL as my focal study site in Palau (Figure 6.1) because recent work (pers. comm., A. Olsen; Olsen *et al.* 2016) has shown that this area supports the largest proportion of breeding Micronesian Megapodes in the archipelago. As a result of logistics, limited time and limited funding, I did not include populations of the subspecies on Peleliu to the south of the RISL, Babeldaob and its offshore islets to the north of the RISL, and Kayangel Atoll to the north of Babeldaob (Figure 6.1). During extensive surveys between 2011 and 2013, Olsen *et al.* (2016) searched 122 individual sites with suitable megapode habitat, between Kayangel Atoll and Peleliu (Angaur was excluded from these surveys), and found 173 active mounds. Eighty-six percent ($n = 149$) of these mounds were found in the Rock Islands area and Kayangel Atoll, the majority ($n = 95$) in the former (92 mounds were found within the actual boundaries of the RISL) (Olsen *et al.* 2016). Thirteen active mounds were found in the Babeldaob area, all on small offshore coastal islets, and 11 were found on Peleliu (Olsen *et al.* 2016), the south-eastern coast of which VanderWerf (2007) had felt supported relatively high densities of the subspecies in 2005. The two most significant breeding populations of the Micronesian Megapode in Palau, therefore, occur in the RISL followed by Kayangel Atoll.

During my field work I located 67 active mounds across 38 separate sites within the boundaries of the RISL, 25 fewer than Olsen *et al.* (2016) had found at 37 sites. As I located the vast majority of these mounds using coordinates collected by the Belau National Museum (pers. comm., A. Olsen), this suggests that 25 previously active mounds had become inactive and had not been replaced since the Olsen *et al.* (2016) surveys, at most six years earlier. This would equate to, and might suggest, at least a 27% decrease in breeding activity by the population of megapodes in the RISL. While this would be cause for concern, a more pragmatic reason for this disparity was the logistical (Appendix A) and onsite physical constraints that precluded me from fully

surveying both the island of Ngerechong and the site Ngeroblobang. At these two sites alone, Belau National Museum (pers. comm., A. Olsen) had found a total of 20 active mounds; because of my lack of time and severe typhoon damage that hampered an effective search, I found five. Adjusting for difference, megapode breeding activity in the RISL may have more realistically decreased by 5–10% since 2013, assuming that the areas I did not search at Ngerechong and Ngeroblobang did not support any active mounds.

Based on the Olsen *et al.* (2016) yield of 173 active incubation mounds in the RISL, this suggests that between 2011 and 2013 there was a breeding population of 346 individual megapodes, assuming no mounds were overlooked. As polygamy is not known to be employed as a breeding strategy by *Megapodius sp.* (Jones *et al.* 1995) this figure may accurately reflect the size of the breeding population. It does not, however, account for the occurrence of non-breeding individuals in the population (i.e., juvenile and sub-adult birds). Through passive surveys of 122 beach sites in the archipelago, Olsen *et al.* (2016) detected 350 individual megapodes at 61 sites, or 5.7 birds per site where birds were detected, but only 2.9 birds across all sites surveyed. Through call-playback surveys, however, I detected 107 individuals at 10 sites (10.7 birds per site, range = 1 – 20 birds per site) in the RISL alone (Table 6.1). This suggests strongly that passive surveys indeed do not yield an accurate count of Micronesian Megapodes in Palau, a conclusion others have come to previously for both this subspecies and the one in the Marianas (e.g., VanderWerf 2007; Amidon *et al.* 2011). Along with 107 detected megapodes, I also located 48 active incubation mounds across these 10 sites, which equates to 2.23 megapodes per mound (Table 6.1). This result likewise suggests that basing surveys of megapodes on the number of active mounds may accurately reflect the size of the breeding population but will underestimate the total population size. Interestingly, on the five islands that were free of tourists the ratio of megapodes to mounds was 1.97, while on tourist-visited islands the ratio was 3.33 (Table 6.1). Given that rats were found to have no effect on megapode relative abundance across islands (Chapter 5), this result does further support my assertion that tourist presence has an adverse effect on megapode breeding in the RISL (Table 6.1).

Table 6. 1. The number of megapodes detected during call playback surveys compared to the number of active incubation mounds on five tourist-visited islands and five islands not visited by tourists in the RISL.

Island	Megapodes Detected	Active Mounds
<i>Tourist-Visited</i>		
Ngeremdiu	1	1
Ioulomekang	3	0
Ulong	19	7
Babelomokang	5	1
Ngchus	2	0
Total	30	9
Mean	6	1.8
<i>Not Tourist Visited</i>		
Dmasech	19	10
Ngeanges	12	7
Lilblau	12	7
Cheleu	14	11
Bailechesengel	20	4
Total	77	39
Mean	15.4	7.8

IUCN Red List Threats to the Micronesian Megapode: Proposed Revisions

The IUCN (2016) lists the Micronesian Megapode as endangered and considers the species susceptible to 11 current threats, nine of which are given an impact score of low and the remaining two of medium (Table 6.2). Two additional threats, (a) volcanic activity and (b) storms and storm induced flooding as a result of climate change, are further considered to be past threats that are likely to re-occur (Table 6.2) (IUCN 2016). The level and degree to which these threats separately affect the two subspecies are considerably different, however. I present these differences in Table 6.3., in which I comparatively assess these threats and propose new rankings for each subspecies based on version 3.2 of the IUCN (2016) Threat Classification Scheme. I also propose an additional climate change related threat (Table 6.3) based on the results of sea level rise modelling that I performed for megapode habitat in the RISL of Palau.

Table 6. 2. IUCN (2016) determined species level threats to the Micronesian Megapode. Under introduced species in the Threat column, 'Unspecified Species' refers to a problematic native species / disease that has not been named or named only at a very general level (IUCN 2016). *Scope* refers to the proportion of the total species population predicted to be affected, and *Severity* refers to the predicted overall population decline caused by a threat.

Threat	Timing	Scope	Severity	Impact Score	Specific Induced Stresses
Hunting and Egg Collecting	Ongoing	Majority (50-90%)	Negligible Declines	Low	Species mortality and reduced reproductive success
Human Recreational Activity	Ongoing	Majority (50-90%)	Slow, Significant Declines	Medium	Species disturbance and reduced reproductive success
Introduced Species					
Goats (<i>Capra hircus</i>)	Ongoing	Majority (50-90%)	Negligible Declines	Low	Ecosystem degradation
Cattle (<i>Bos Taurus</i>)	Ongoing	Majority (50-90%)	Negligible Declines	Low	Ecosystem degradation
Pigs (<i>Sus domesticus</i>)	Ongoing	Majority (50-90%)	Negligible Declines	Low	Ecosystem degradation and reduced reproductive success
Black Rats (<i>Rattus rattus</i>)	Ongoing	Majority (50-90%)	Negligible Declines	Low	Reduced reproductive success
Norway Rat (<i>Rattus norvegicus</i>)	Ongoing	Majority (50-90%)	Negligible Declines	Low	Reduced reproductive success
Dogs (<i>Canis familiaris</i>)	Ongoing	Majority (50-90%)	Negligible Declines	Low	Species mortality
Cats (<i>Felis catus</i>)	Ongoing	Majority (50-90%)	Negligible Declines	Low	Species mortality
Brown Treesnake (<i>Boiga irregularis</i>)	Future	Majority (50-90%)	Very Rapid Declines	Medium	Species mortality
Unspecified Species	Ongoing	Minority (<50%)	Negligible Declines	Low	Species mortality
Geological and Climatic					
Volcanoes	Past, likely to return	Minority (<50%)	Rapid Declines	Past	Ecosystem conversion and degradation
Storms and Flooding	Past, likely to return	Minority (<50%)	Could Cause Fluctuations	Past	Ecosystem degradation

Table 6. 3. Proposed revision to IUCN (2016) listed threats to the Micronesian Megapode as presented in Table 6.2., and a comparison of these threats by subspecies. TCL = IUCN Threat Classification Level; IS = Impact Score, as calculated based on Version 1.0 of the IUCN (2016) Threat Impact Scoring System.

Megapodius laperouse laperouse										Megapodius laperouse senex				
Threat	TCL	Timing	Scope	Severity	IS	Timing	Scope	Severity	IS					
Hunting and Egg Collecting	5.1.1.1	Past, unlikely to return	Unknown	No Declines	No Impact	Ongoing	Minority	Negligible	Low					
Human Recreational Activity	6.1	Ongoing	Minority	Negligible	Low	Ongoing	Majority	Slow, Significant	Medium					
Introduced Species														
Goats (Capra hircus)	8.1.2	Ongoing	Minority	Negligible	Low	Future	Minority	Negligible	Low					
Cattle (Bos Taurus)	8.1.2	Ongoing	Minority	Negligible	Low	Future	Minority	Negligible	Low					
Pigs (Sus domesticus)	8.1.2	Ongoing	Minority	Negligible	Low	Ongoing	Minority	Negligible	Low					
Black Rats (Rattus rattus)	8.1.2	Ongoing	Majority	Negligible	Low	Ongoing	Majority	Negligible	Low					
Norway Rat (Rattus norvegicus)	8.1.2	Ongoing	Minority	Negligible	Low	Ongoing	Majority	Negligible	Low					
Dogs (Canis familiaris)	8.1.2	Ongoing	Minority	Negligible	Low	Ongoing	Minority	Negligible	Low					
Cats (Felis catus)	8.1.2	Ongoing	Minority	Negligible	Low	Ongoing	Majority	Very Rapid	High					
Brown Treesnake (Boiga irregularis)	8.1.2	Future	Minority	Very Rapid	Low	Future	Minority	Negligible	Low					
Crab-eating Macaque (Macaca fascicularis)	8.1.2	NA	NA	NA	NA	Ongoing	Minority	Negligible	Low					
Mangrove Monitor Lizard (Varanus indicus)	8.1.2	Ongoing	Minority	Negligible	Low	Ongoing	Majority	Negligible	Low					
Geological and Climatic														
Volcanoes	10.1	Past, likely to return	Majority	Rapid	Low	Past, unlikely to return	Unknown	No Declines	No Impact					
Sea Level Rise (Breeding Habitat Inundation)	11.1	Future	Minority	Negligible	Negligible	Future	Majority	Slow, Significant	Low					
Storms and Flooding	11.4	Ongoing	Majority	Fluctuations	Low	Ongoing	Majority	Fluctuations	Low					

The IUCN (2016) suggests that the anthropogenic threats of hunting, egg collecting, and disturbance by recreational activities affect the majority of the species' population (Table 6.2). Although hunting of megapodes likely rarely occurs any longer in either the Mariana Islands or Palau, egg collecting at incubation mounds by the local populace in the latter is known to be ongoing (Table 6.3) and to be practiced on a very limited basis (Engbring 1992; pers. comm., C. Kitalong). Egg collecting on islands north of Saipan in the Mariana archipelago was documented as recently as the late 1970's (Ludwig 1979) but there are no records or observations of its occurrence since (USFWS 1998; Amidon *et al.* 2011). While egg collecting may affect the minority of the population in Palau and lead to negligible declines, this activity likely has no real impact on the population in the Mariana Islands (Table 6.3).

Human recreational activities are suggested to be potentially responsible for a slow but significant decline in the species' population and is given an impact score of medium by the IUCN (2016) (Table 6.2). This threat, however, realistically affects the megapode in Palau more so (Table 6.3), where dive operators and their clientele routinely use beaches in the RISL where the majority of the archipelago's breeding population is known to occur (Chapter 5). I found detection rates for megapodes on tourist-visited islands to be significantly lower than on islands not visited by tourists, suggesting that human presence affects the behaviour of birds on the former (Chapter 5). Tourist-visited islands also supported 30% fewer active mounds than islands not visited by tourist (Table 6.1), and the ratio of megapodes to active incubation mounds was lower on the former compared to the latter (1.97 vs 3.33 birds per active mound). This suggests that high levels of human presence have a negative effect on megapode breeding in Palau. Nonetheless, although there are as many as 38 beaches in the RISL on which megapodes occur and breed (Chapter 4; Olsen *et al.* 2016), tourists routinely and heavily make use of only seven at the current time (pers. obs., P. Radley). I have therefore not increased the IUCN (2016) designated impact score for this threat of 'Medium' for the population in Palau (Table 6.3).

Although the vast majority of megapodes in the Marianas occur on the distant, mostly uninhabited islands north of Saipan that are well out of reach of regular tourist activities, they are very infrequently visited by birding and ecotourism groups on large cruise vessels (with explicit permission from the local governing body, the Commonwealth of the Northern Mariana Islands or CNMI; pers. obs., P. Radley).

Affected more so may be the small population of megapodes that occur on Saipan, where they are found mostly in the northern areas of the island that support pockets of native forest. Hiking trails are cut through much of these forests, and a mountain biking trail was surreptitiously established in 2010 and / or 2011 (pers. obs., P. Radley). These trails and birding / ecotourism cruises may bring humans into relatively infrequent contact with a small minority of megapodes in the Mariana Islands, leading to at most a negligible impact on their overall population in the archipelago (Table 6.3).

Aside from the brown treesnake (*Boiga irregularis*), all introduced species that are named by the IUCN (2016) (Table 6.2) are indicated to affect the majority of the species' population, and all are considered to be responsible for negligible declines in its population. Feral ungulates (i.e., cattle, goats, and pigs) currently occur on five islands in the Mariana archipelago that support megapodes and the resulting alteration of habitat by these introduced ungulates may be detrimental to populations of the bird that occur on them (Amidon *et al.* 2010; Amidon *et al.* 2011). Ungulates are not found on the Mariana Islands of Asuncion, Guguan, and Sarigan (Figure 6.1), however, which cumulatively support 87% of the estimated megapode population in the archipelago (Amidon *et al.* 2011). Asuncion and Guguan are CNMI designated conservation islands that have historically been exposed to very little human presence and to which ungulates were never introduced (Berger *et al.* 2005). Sarigan, for which conservation island status has been proposed, once supported a population of feral goats and pigs that were eradicated in the late 1990's as part of a U.S. Department of Defence funded mitigation initiative (Kessler 2002). The ongoing presence of introduced goats, cattle and pigs, therefore, affect only a minority of the megapodes in the Marianas and would likely cause only a negligible decline in the species' population in the archipelago (Table 6.3).

Although ungulates are not documented as having an effect on megapodes in Palau, and are not present in the RISL, very little is known about the extent of feral establishment of these introduced species in the archipelago. Efforts to introduce goats and cattle for agricultural livestock purposes were attempted in the 1970's (pers. comm., J. Miles [Division of Fish and Wildlife Protection, Palau]). Aside from a few local families keeping penned goats on their land and a small number of managed cattle in one small area of Babeldaob, however, these attempts were ultimately not successful and no feral population of either is known to occur in the archipelago (pers. comm., J. Miles). As these two ungulate species are present on Babeldaob, they may serve as a

potential future threat to megapodes only on this island, but would result in negligible declines in the total megapode population of Palau (Table 6.3). A population of feral pigs is only known to exist on Babeldaob but the extent of their range across the island is unknown and the level of damage caused by them is currently not thought to be extensive (pers. comm., J. Miles, T. Hall [Island Conservation], G. Wiles, and A. Olsen). Given their restriction to Babeldaob, pigs are an ongoing threat to a small portion of megapodes in Palau and, like goats and cattle, would have minimal impact on the overall megapode population in the archipelago (Table 6.3).

The black rat (*Rattus rattus*), named as one of two rodent threats to megapodes in Table 6.2, does occur in the RISL (Chapter 5; pers. comm., T. Hall). My findings presented in Chapter 5 suggest, however, that rats are not a major threat to mound nesting Micronesian Megapodes in the RISL. For similar reasons, they would likely have little effect on populations of nesting megapodes in the Marianas. Based on the complications experienced during my second field season (Appendix A), however, further investigations should be conducted to confirm that introduced rats indeed do not have a detrimental effect on megapodes. While the IUCN (2016) considers the Norway rat (*Rattus norvegicus*) a threat to megapodes in the Marianas (Table 6.2), this species comprised only 0.7% of the combined sample of three rat species caught ($n = 728$) during a survey of rodents on Rota, Tinian, and Saipan by Wiewel *et al.* (2009), and only *R. rattus* was caught by Adams *et al.* (2010) on Pagan (Figure 6.1). Similarly, in Palau, although the Norway rat is known to occur in the RISL, it likely occurs in relatively low densities (pers. comm., T. Hall). This further and strongly suggests very little to no possible effect of *R. norvegicus* on either subspecies of the Micronesian Megapode (Table 6.3). Black rats, however, I consider an ongoing threat that my findings suggest may lead to negligible declines in megapode populations in both Palau and the Marinas, but the impact score for this threat remains at the IUCN (2016) designation of ‘Low’ until further investigation is completed (Table 6.3).

Introduced dogs and cats are known to have serious consequences for populations of other species of megapodes (Jones *et al.* 1995; Dekker *et al.* 2000) and the IUCN (2016) considers both a threat to the majority of the Micronesian Megapode population (Table 6.2). In the Marianas, like feral ungulates these introduced predators are only known to occur on islands that are or were once inhabited by humans (Amidon *et al.* 2011). In terms of the megapode’s effective range in the archipelago, dogs have

only been recorded on Saipan, Alamagan, and Agrihan (Figure 6.1) (Amidon *et al.* 2011), on the latter of which Ludwig (1979) observed feral dogs raiding megapode incubation sites. Cats occur on these same islands and observations of them have been made on Sarigan, the island on which occurs the second greatest abundance of megapodes in the archipelago (Amidon *et al.* 2011). Regardless, 72% of the megapode population in the Marianas occurs on islands known to be free of this highly detrimental introduced carnivore (Amidon *et al.* 2011). Dogs and cats, therefore, are ongoing threats to the minority of megapodes in the Mariana Islands and will likely have only a low or negligible impact on the population in the archipelago (Table 6.3).

In Palau, feral dogs are not apparently widespread and primarily occur as stray individuals in and around villages mostly on Babeldaob (pers. comm., A. Olsen, J. Miles, and T. Hall). They would thus serve as an ongoing threat to only a very small minority of megapodes and have a negligible impact on the population as a whole (Table 6.3). Feral cats, on the other hand, are very common on Babeldaob, where the People and Animal Welfare Society (PAWS) is currently conducting an evaluation of their numbers and environmental impact (pers. comm., J. Miles and T. Hall). Feral cats are also known to be present and reproducing on Kayangel, and are known to occur at Ngeremdiu and Ngchus on the large island of Ngeruktable in the RISL (pers. comm., T. Hall and J. Miles). During field surveys for megapodes, my field assistant (M. Lohr) and I found the well decomposed remains of a megapode at Ngchus, but we were not able to positively confirm the cause of its death. Introduced cats are well documented as a serious threat to island ecosystems where they have a devastating effect on native and endangered vertebrate taxa (e.g., Medina *et al.* 2011; Nogales *et al.* 2013; Doherty *et al.* 2016). Cats are thus certainly an ongoing threat to the majority of megapodes in Palau, and one that could have a serious effect on the population (Table 6.3).

Crab-eating macaques (*Macaca fascicularis*) were introduced to Angaur in Palau by German phosphate miners in the early 1900's (Poirier & Smith 1974). The IUCN (2016) does not include the macaque on their list of introduced threats to megapodes (Table 6.2) and the species is known to mostly consume plant-based foods on Angaur (Poirier & Smith 1974). The macaque's opportunistic and aggressively omnivorous behaviour, however, may cause them to be a threat to megapodes on the island (pers. comm., J. Miles and T. Hall). As they only occur on Angaur they are an

ongoing threat to only a minority of the megapode in the archipelago and would be responsible for only a negligible decline in the overall population (Table 6.3).

There is much debate whether mangrove monitor lizards (*Varanus indicus*), which occur in both the Mariana Islands and Palau, are introduced or endemic to the two archipelagos. While the Japanese had introduced the lizard to other islands in the Pacific as biological pest control (pers. comm., T. Hall), evidence suggest this was not the case in the Marianas and that the species either arrived by natural dispersal or was introduced prior to Western or Japanese presence in the archipelago (Cota 2008). Pregill and Steadman (2009) assert that monitor lizards were introduced to Guam no later than 1600. Local residents and government officials in Palau, however, insist the species is recently introduced and invasive in the archipelago, but science suggests that they are more likely native to the islands (Crombie & Pregill 1999; pers. comm., T. Hall and J. Miles). Regardless, given the indecision and potential pre-European introduction to the Marianas, I consider them an introduced species in Table 6.3. Monitor lizards have been observed raiding megapode incubation sites in both archipelagos and consuming an adult bird on Sarigan in the Marianas (pers. comm., T. Hall; Ludwig 1979). Although they are considered a likely threat to megapodes (pers. comm., T. Hall; USFWS 1998), and these observations confirm that, evidence also suggests that predation by monitor lizards is relatively rare (e.g., Olsen *et al.* 2013). In the Marianas, the lizard occurs on all islands except FDM, Guguan, Asuncion, Maug, and Uracas (Vogt 2010), and therefore will affect a minority (at most 28%) of megapodes in the archipelago (Amidon *et al.* 2011) and have a negligible impact on their population (Table 6.3). In Palau the species apparently occurs on most islands (pers. comm., T. Hall) and will thus affect the majority of megapodes. As monitor lizards may be native to these islands, they would likely have only a negligible impact on megapode populations in the archipelago (Table 6.3).

The IUCN (2016) proposes that a possible future introduction of the brown treesnake would likewise affect the majority of Micronesian Megapodes and would produce a very rapid decline of its population; this threat is given an impact score of medium (Table 6.2). This introduced snake quickly devastated Guam's bird life (Savidge 1987; Wiles *et al.* 2003) and is considered the greatest threat to the avifauna of the CNMI (the political affiliation of all 14 islands north of Guam), where an incipient population of the brown treesnake is thought to occur (Colvin *et al.* 2005). It is equally

a threat to other Pacific islands that receive air and / or sea freight from Guam (Colvin *et al.* 2005), which does include Palau where the snake is currently absent (Rodda & Savidge 2007). Unlike the islands of the Mariana archipelago, however, other species of bird-eating snakes do naturally occur in Palau and its avifauna is likely behaviourally adapted to this threat (Rodda & Savidge 2007). Given this, and the effective brown treesnake interdiction program in place on Guam (Rodda & Savidge 2007), this introduced species remains a future threat to megapodes in Palau that would have a negligible impact on the species population in the archipelago (Table 6.3). In the Marianas the brown treesnake is primarily a threat to the avifauna of the human populated islands of Rota, Tinian, and Saipan (Colvin *et al.* 2005). As the vast majority of megapodes occur on the seldom visited islands north of Saipan, which are considered to be safe from the threat of the treesnake (MAC Working Group 2014), this population would likewise be little affected by the introduced snake, and I have given this threat in the Marianas an impact score of ‘Low’ (Table 6.3). Regardless, the IUCN (2016) considers the megapode and other avian species in the Marianas Islands potentially at risk owing simply to the proximity to Guam of the majority of its population, the source of the threat of the brown treesnake

The IUCN (2016) predicts volcanic activity and storms and flooding to affect only a minority of the entire Micronesian Megapode population (Table 6.2). Volcanism, which facilitates breeding by a large portion of megapodes in the Mariana islands (Glass & Aldan 1988; Jones *et al.* 1995), is only a potential but real threat to the subspecies in this archipelago. Whereas all islands north of FDM in the Marianas (where the majority of the world’s Micronesian Megapodes occur) are relatively young and are either active or dormant volcanos (Bloomer *et al.* 1989), the volcanically derived islands in Palau are ancient remnants of a once active past (Kitalong 2014). Based on population estimates for the Mariana archipelago by Amidon *et al.* (2011), serious if not cataclysmic volcanic eruptions by either Asuncion or Sarigan could affect more than a minority of the Micronesian Megapode population, as is suggested by the IUCN (2016). As an example of this threat, the relatively small population of megapodes that once occurred on Anatahan (Figure 6.1) (Curz *et al.* 2000) is believed to have been driven or extirpated from the island as a result of a series of substantial and drastic habitat altering eruptions between 2003 and 2005 (Amidon *et al.* 2011). Where volcanic activity is therefore not a real threat to megapodes in Palau, it is a very real but

unpredictable threat to the population in the Marianas where it would cause a relatively rapid population decline that would be isolated to the affected island (Table 6.3). This, however, is a threat the species has faced since it established itself in the Marianas, and one to which it is very likely well adapted, leading to an impact score of ‘Low’.

The IUCN (2016) suggests that the Micronesian Megapode in the Mariana and Palau archipelagos are both equally threatened by increased storm / typhoon intensity as a result of climate change (Table 6.2). Megapodes in the Mariana Islands, however, are currently not known to breed at an elevation that is within close proximity to the ocean (Jones *et al.* 1995) and therefore would likely be little threatened by the tidal surges generally associated with large storms such as typhoons. The forested areas and habitat in which they occur and breed can be and frequently are affected by the exceedingly damaging winds that are generated by such storms (Berger *et al.* 2005; Ha *et al.* 2012). In Palau, however, not only can relevant habitat be devastated by powerful winds, but the vast majority of megapodes are known to breed in littoral habitat that is just above high tide (Chapter 3 and 4), where they can be heavily impacted by storm surge (Olsen *et al.* 2013; Olsen & Eberdong 2013; Olsen *et al.* 2016). Increased storm frequency and intensity as a result of climate change is an ongoing threat in both archipelagos that affects the majority of megapodes in each, and that will likely cause fluctuations in their populations (Table 6.3). Although large, damaging storms are far more common in the Marianas than Palau (Berger *et al.* 2005; pers. comm., A. Olsen), they are climatic phenomena to which megapodes in both archipelagos have long been exposed (Spennemann 2004), and to which they have likely evolved some resilience.

As I showed in Chapter 4, megapodes in Palau are highly threatened by climate change driven sea level rise given their tendency to breed in habitat in the archipelago that is most susceptible to inundation. The IUCN (2016), however, does not currently consider sea level rise a threat to the Micronesian Megapode (Table 6.2). I therefore propose that Sea Level Rise (Breeding Habitat Inundation) be included for the species (Table 6.3) under threat classification 11.1 Habitat Shifting and Alteration (under the category heading ‘Climate Change and Sever Weather’) following Version 3.2 of the IUCN (2016) ‘Threats Classification Scheme’. The modelling I performed in ArcGIS to assess the scope of climate change driven sea level rise on the subspecies in the RISL showed that between 32% and 43% of its current breeding habitat would be inundated during twice-daily high tides (Chapter 4). Given the shortcomings I uncovered in the

elevation data I used, this estimate may very well be conservative and much more breeding habitat may be lost. As the second largest portion of the population in Palau occurs in the equally low-lying littoral strand habitat of Kayangel Atoll (Olsen *et al.* 2016), loss of breeding habitat there would likely be comparable to that lost in the RISL. The majority of megapodes in the archipelago are therefore at threat by sea level rise caused inundation, which would likely lead to slow but significant declines in the population over the long term (Table 6.3). For the same reason that megapodes in the Mariana Islands would not be as heavily affected by tidal surges during storms, a minority in the archipelago would be impacted, resulting in negligible declines in this population (Table 6.3). In terms of the threat of sea level rise at the species level, based on population estimates of the species for the two archipelagos (Engbring 1992; Amidon *et al.* 2011; Olsen *et al.* 2016), only a relative minority of the world's Micronesian Megapode population would be affected by climate change induced inundation of breeding habitat.

An Overlooked Threat; The Paucity of Data

With a total land area of less than only 47,000 km², the tropical Pacific of Oceania supports 187 endemic species of landbirds, and with an average species density 53 times greater than that of the world's continents, holds the greatest density of avian species on the planet (Newton 2003). However, birds of this region (excepting Hawai'i) are relatively very understudied. Perhaps one of the more profound, but lesser discussed or appreciated obstacles to conservation of landbirds in the tropical Pacific is the paucity of data for the vast majority of them, including the Micronesian Megapode in Palau, regarding various aspects of their life history and ecology. Steadman (2006) decries this lack of data and the relative little attention paid to the tropical Pacific by both researchers and governmental funding agencies, and calls for further research into population trends, nesting ecology, habitat preferences, food habits and potential vulnerabilities of landbirds of the region.

In this thesis, I have endeavoured to fill some of these gaps in knowledge for one population of one species of landbird in Micronesia. During my previous tenure as a biologist with the CNMI's Division of Fish and Wildlife on Saipan, I had likewise done what I could to increase the quality of data already being collected for endemic

landbirds on three islands in Mariana archipelago (e.g., Ha *et al.* 2018). I also strove to further increase knowledge of them by collaboratively developing and initiating more intensive research and monitoring projects (e.g., Saracco *et al.* 2014; Saracco *et al.* 2016). Researchers and practitioners involved in other areas of the tropical Pacific are likewise doing their parts (e.g., pers. comm., A. Olsen [Belau National Museum], M. O'Brien [BirdLife International Fiji]), but compared to the earth's more populated and more readily and cost effectively accessible continental landmasses, this is only a beginning in terms of what needs to be done.

My project highlights another form of important data that is currently and greatly lacking: relevant, high resolution digital spatial data necessary for modelling the effects of climate change and sea level rise on terrestrial ecosystems in the Pacific (pers. comm., F. Amidon [U.S. Fish and Wildlife Service], P. Berkowitz [U.S. Geological Survey], and M. Kottermair [University of Guam]). This includes a lack of both topographic surface and elevation data as well as accurate and effective digital habitat cover data. Exceptions to this include some island nations that are affiliated or otherwise supported by other resource rich, developed nations, or that serve as strategic or economic importance to other developed nations. Fortunately, for the needs of my project, Palau falls into one of the latter categories. Once a protectorate of the United States, Palau now has a "Compact of Free Association" with this nation, which has agreed to come to Palau's protection in time of military hostility and provide economic and humanitarian assistance as needed (USDoS 1986). The United States also has federal branch field offices located in Palau including those of the U.S. Department of Agriculture. Thus, while high resolution habitat data are still needed for much of this island nation, relatively high quality topographic / elevation layers do exist. This is a recent development, however, and the same cannot be said for the majority of other sovereign island nations in the Pacific.

Although Vricon digital spatial layers are overall quite good, my work in this thesis does point to a critical shortcoming of these data in terms of the exaggerated rendering of elevations in their elevation model (i.e., Digital Terrain Model or DTM) that I used for sea level rise analysis. As I showed in Chapter 4, they are arguably the best elevation models currently available for Palau. They are based on the latest commercial satellite imagery and produced by a unique process that employs industry-leading, automated 3D modelling algorithms (Vricon 2017; pers. comm., C. Brower).

This is a drastic improvement over the USGS DEMs, which were produced by essentially digitizing the elevation contours from USGS topographic quadrangle maps that were originally produced via an analogue process based on high altitude acquired aerial images dating to around 1970 (Osborn *et al.* 2001; pers. comm., F. Amidon). Elevation data acquired by either Light Detection and Ranging (LiDAR) technology or Interferometric Synthetic Aperture Radar (IFSAR), however, would be a major advantage and would facilitate the most accurate DEM creation for sea level rise modelling and assessment (Fraser & Ravanbaksh 2011). LiDAR is preferred in coastal areas owing to its multiple-return / pass capability that allows for more accurate filtering out of vegetation and more refined and accurate elevations when converting from the initially acquired Digital Surface Model (DSM) to the bare-earth DEM (Fraser & Ravanbaksh 2011). The confounding factor of these technologies, however, is their cost, which is prohibitive for small island nations that simply do not have the financial means to prioritize their acquisition in their annual operational budgets (pers. comm., M. Kottermair and M. Aurelio).

Conclusion: Research Needs for Conservation of the Micronesian Megapode in Palau

Both throughout the preceding chapters of my thesis and in the above Synthesis sections, it is readily apparent that further research and data are necessary to fully understand the conservation needs of the Micronesian Megapode in Palau. Based on my experience with the species as a whole (in both the Marianas and Palau), my findings on megapodes in Palau and experience with that archipelago, and my comprehensive review of literature for this thesis, I suggest the following as research and data acquisition priorities:

- ***Intensive surveys for “atypical” megapode mounds and / or evidence of alternate incubation strategies.*** Extensive searches should be conducted on both Babeldaob and in all upland areas of the RISL. Surveys of these hard to reach and little inspected areas of the archipelago, although physically demanding and time consuming, would shed light on their current importance to megapodes and help to determine a more accurate estimate of the breeding population.

- ***Long-term remote trail-camera observation of incubation mounds in Palau.*** Setting remote cameras at mounds for a year or more would help to pin down the approximate timing and duration of annual breeding by megapodes. This information could be used to guide the timing of other research, such as call-playback surveys, and may possibly help to shed light on megapode fecundity in the archipelago.
- ***Call-playback surveys for Micronesian Megapodes on all major islands and / or island areas in Palau.*** Call playback surveys would yield a more robust picture of the number of adult megapodes in Palau, by island or island group, including an estimate of non-breeding individuals. Although these data could not be used to generate DISTANCE estimated total abundance (Buckland *et al.* 2001), they could be used to calculate more accurate occupancy and station level relative abundance estimates for the subspecies.
- ***Comprehensive surveys for feral ungulates (goats, pigs, and cattle), dogs, and cats on all islands or island areas that support megapodes (Kayangel, Babeldaob, RISL, Peleliu, and Angaur).*** Although these invasive taxa can have serious consequences for native terrestrial habitat and vertebrate fauna, a full assessment of their presence and population status have not yet been executed for the entire archipelago (pers. comm., J. Miles). This would allow for fully gauging the extent of their potential threat to megapodes and other sensitive species of vertebrate taxa. As they have been observed at two beaches, the most important such survey may be a full exploration of the RISL for feral cats, given the level of threat they pose to all birds and other vertebrates within the conservation area.
- ***Further study of the effect of rats and tourists on megapodes in Palau.*** Continued and repeated call playback surveys of megapodes would allow for estimates of occupancy for them, and a direct comparison with my current occupancy estimates for rats. Continued monthly surveys for both rats and megapodes over the duration of a year or more would allow for factoring variables such as seasonality into more robust estimates. Lastly, to investigate the relative impacts of rats and tourist presence on megapodes, rats should be experimentally removed from both tourist-visited and tourist-free islands (in cooperation with Island Conservation) and the response of megapodes measured and assessed.

- ***Collection of megapode blood samples, or alternative genetic material, from all islands in Palau on which megapodes occur.*** This would facilitate the assessment of the level of dispersal and gene flow of megapodes throughout the archipelago, and shed light on genetic connectivity and mixing between birds from different islands groups.
- ***VHF or satellite based telemetry study of megapodes in Palau.*** An intensive telemetry based study would yield valuable information on the current level, degree, and distances of inter-island movements by megapodes in the archipelago. This would hint at their ability to flee to more distant higher ground and perhaps to the possibility of their using Babeldaob as refuge from sea level rise.
- ***Acquisition of LiDAR data for Palau.*** Although expensive to acquire, these data would allow for a more accurate, full, and nuanced assessment of the possible effect of sea level rise on megapodes and other birds and wildlife in the archipelago.

The Micronesian Megapode in Palau shares intrinsic biological and ecological traits with other species of megapode that rank as the most vulnerable to climate change as a whole (Radley *et al.* 2018). This subspecies is relatively rare, is apparently a habitat specialist, is confined to a highly restricted range, and is also moderately to highly isolated owing to its endemism to a small archipelago in the Pacific. My findings further suggest that this subspecies is also moderately to highly threatened by rising seas (Chapter 4). While this subspecies is exposed to most of the same IUCN (2016) listed threats (Table 6.3) as the subspecies in the Mariana archipelago, the population in Palau is likely more at risk because of heavy tourist presence in its preferred breeding habitat (Chapter 5) and the presence of introduced cats that potentially occur on islands in the archipelago that are important to megapodes. However, the megapode in Palau is much less well surveyed and its status much less known or certain than the subspecies in the Mariana Islands (Amidon *et al.* 2011). The research and data needs that I propose above would help to fill these gaps in knowledge of the Micronesian Megapode in Palau, while also increasing the insight into its life history that is necessary to inform efforts towards its long-term conservation and protection.

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APPENDICES

Appendix A. Challenges Encountered During Field Work in Palau

Appendix B. Trait-based Vulnerability Assessment; Supplementary Material for Chapter 2

APPENDIX A: Challenges Encountered During Field Work in Palau

Research in remote and foreign locations presents often unique, numerous, and varied challenges. Amongst these, particularly as a postgraduate student, is stretching especially limited funds to acquire the data necessary to meet project objectives. My advisor, Rob Davis, and I had entered into this project as a collaboratively facilitated field effort with the Koror State Government's (KSG) Rangers. They kindly provided all boat transportation for my first field season to and within the Rock Island Southern Lagoon Conservation Area (RISL), as well as an assistant (Philip Terenciano) to help with data collection. The Rangers kept a tight schedule, however, and my time in the field was limited to what their daily routines and work schedules could facilitate. Consequently, the islands I had access to were mostly those along their regular patrol routes in the RISL. Their ability to take me to some of these islands was further dictated by tides and seasonal water conditions.

An active and busy schedule precluded the Rangers from assisting me during my second season, a situation I was not aware of until I arrived in Palau to begin my second round of data collection. The field effort of my second season was only made possible by a small grant of \$5000 (USD) that I received last minute from the World Pheasant Association, and the generosity, time, and vast knowledge of my local boat operator Mr. Clarence Kitalong. Altogether, these funds and an additional \$1000 (AUD) received from the ECU School of Science, paid for 19 days of boat transport. Mr. Kitalong was fully paid for his services with these monies, but he often went over his normal daily operational time limit to accommodate me and never balked at my needs or requests.

Ultimately, a lack of autonomy hampered my ability to effectively collect data during my first field season. This negated my ability to start field work at an early hour of my choosing, limited the amount of time I spent in the field on a daily basis, and restricted the number of islands to which I had ready access. It also hampered my ability to make last minute schedule changes, as field conditions often warrant. Regardless of these limitations, I feel that I obtained solid data necessary to shed light on the habitat requirements and climate change related conservation issues that the

relatively little studied Micronesian Megapode (*Megapodius laperouse senex*) faces in Palau. The results of my work are detailed in the chapters of this thesis. The following, however, are the areas where I feel that I came up short in terms of data collection, and which prompted relatively last minute changes to my methods of data collection.

Incubation Mound Habitat Data Collection (Chapter 3)

Collection of habitat data at megapode incubation mounds was affected most by the lack of autonomy during my first field season. Limited funds lead me to rely solely on the busy staff of the KSG Rangers for boat transportation. This reliance ultimately limited my time in the field and the islands to which I had access in the RISL. At our most efficient, habitat data collection took my assistant and I about 1.75 hours per mound with random point combined. On our longest days, we usually managed to collect data at three mounds and two-to-three random points. However, as many islands known to support megapode breeding were outside of the daily routes of the Rangers' patrols, we quickly depleted the number of active mounds available to us. To reach mounds on other, relatively more distant islands, it was required that I submit a request to the KSG Chief Ranger. Such requests were generally granted but my time on these islands was especially limited because they were all well off the Rangers' patrol routes. In such instances I was forced to focus specifically on gathering mound location data for sea level rise modelling (Chapter 4), as opposed to spending time collecting habitat data on only a relative few mounds.

Megapode Surveys (Chapter 5)

The lack of a repeat sample for my megapode surveys caused the calculation of their detection probability to be impossible, thus rendering occupancy analysis likewise not possible with the data that I collected for the species in the (RISL). Call playback surveys used for collecting these data were relatively time consuming and labour intensive, especially when conducted with only one assistant and from one small boat over an expansive area such as the RISL. Logistics and competing research / data needs during my abridged second field season prevented me from completing more than one survey. If I had tried to squeeze a repeat survey into my brief second season, visits to

islands would have been separated by only eight to 10 days at most. In hindsight, however, this may have been better than acquiring only one sample of data. Although I did not have these surveys planned as part of my first field season, if I had, I would have then been hampered by the aforementioned lack of autonomy to move about the RISL as needed and to execute counts when most beneficial in the early morning hours.

Adult Dispersal and Gene Flow

As detailed in my research proposal, I had originally intended to employ radio-telemetry to document and investigate inter-island movement of adult megapodes in the RISL. I had also intended to use contemporary molecular techniques to determine genetic connectivity within the RISL population. Aside from a need for significantly more funding than I had, both activities would have required a great deal of time and autonomy to collect adequate data and achieve significant results. Although I was initially willing to attempt collecting these data with the funds Rob Davis and I had acquired, I abandoned both efforts in part because of the lack of time and freedom of movement resulting from our reliance on the KSG Rangers for transportation in the RISL.

APPENDIX B: Trait-based Vulnerability Assessment;

Supplementary Material for Chapter 2

In the following, Tables B1–B6 were used to score sensitivity, exposure, adaptive capacity, other extrinsic threats to, and conservation actions for, the world’s megapodes as investigated in Chapter 2. Scoring for all but exposure (Table B2) was facilitated by data presented in Tables B7–B13, which were populated through exhaustive literature review for the Megapodiidae (Table B14), which included the accounts for each species at the IUCN (2016) Red List of Threatened Species. Exposure was assessed with calculate change values in Table B15. Species are denoted by the following four-letter codes:

MOME = Moluccan Megapode (*Eulipoa wallacei*)
SUME = Sula Megapode (*Megapodius bernsteinii*)
PHME = Philippine Megapode (*Megapodius cumingii*)
NGME = New Guinea Megapode (*Megapodius decollatus*)
MEME = Melanesian Megapode (*Megapodius eremita*)
DUME = Dusky Megapode (*Megapodius freycinet*)
BIME = Biak Megapode (*Megapodius geelvinkianus*)
MIME = Micronesian Megapode (*Megapodius laperouse*)
VAME = Vanuatu Megapode (*Megapodius layardi*)
NIME = Nicobar Megapode (*Megapodius nicobariensis*)
POME = Polynesian Megapode (*Megapodius pritchardii*)
OFME = Orange-footed Megapode (*Megapodius reinwardt*)
TAME = Tanimbar Megapode (*Megapodius tenimberensis*)
MALE = Maleo (*Macrocephalon maleo*)
WABT = Wattled Brush-Turkey (*Aepypodius arfakianus*)
WGBT = Waigeo Brush-Turkey (*Aepypodius bruijnii*)
AUBT = Australian Brush-Turkey (*Alectura lathami*)
MALL = Malleefowl (*Leipoa ocellata*)
RBBT = Red-billed Brush-Turkey (*Talegalla cuvieri*)
BBBT = Black-billed Brush-Turkey (*Talegalla fuscirostris*)
COBT = Collared Brush-Turkey (*Talegalla jobiensis*)

Habitat Codes used in Table B9

Forested Cover: MM = Moist Montane Forest; ML = Moist Lowland Forest; SW = Swamp / Wetland Forest; D = Dry Forest; T = Temperate Forest; SM = Supratidal Mangrove Forest; De = Degraded Forest.

Savanna and Wetlands: DS = Dry Savanna; IW = Inland Wetland.

Scrublands: M = Moist Scrubland; D = Dry Scrubland.

Shrub-lands: D = Dry Shrub-land; M = Moist Shrub-land, T = Temperate Shrub-land.

Other Cover Types: CS = Coastal Supratidal; PA = Plantation / Agriculture; RG = Rural Areas / Gardens.

Codes used for Extrinsic Known Threats in Table B10

Deterministic Threats: Def = Deforestation; HF = Habitat Fragmentation; FDD = Forest Degradation / Destruction; ASF = Agriculture / Subsistence Farming; EC = Egg Collecting / Overharvesting; Hun = Hunting; IP = Introduced Predators; IC = Introduced Ungulates / Feral Competitors.

Stochastic Threats: V = Volcanic Activity; F = Fire; T/C = Typhoon / Cyclone.

Codes used for Current and Proposed Conservation Actions in Tables B11 and B12.

LP = Local or Legal Protection; HM = Hunting / Harvesting Management; SR = Nesting Status / Surveys or Research; TR = Egg Translocation / Reintroduction; HP = Nesting / Foraging Habitat Protection; SC = Invasive / Introduced Species Control; CP = Conservation Plan Drafted; EP = Education Programs established.

Table B 1. Trait groups, relevant traits, and scoring for level of sensitivity of megapodes to the manifestations of climate change. These data were gleaned through review of published literature presented in Table B14. Species for which data are deficient is indicated with “dd”.

SENSITIVITY				Scrubfowl Clade														Brush-Turkey Clade						
Trait Group	Trait	Scoring	Tot. pos.	MO ME	SU ME	PH ME	NG ME	ME ME	DU ME	BI ME	MI ME	VA ME	NI ME	PO ME	OF ME	TA ME	MA LE	WA BT	WG BT	AU BT	MA LL	RB BT	BB BT	CO BT
Habitat Specialist	Habitat plasticity	1 = utilizes ≥4 habitats 2 = utilizes 2–3 habitats 3 = utilizes 1 habitat	3	2	1	2	2	2	1	1	1	3	3	3	1	2	1	3	2	1	1	2	1	2
		1 = >100,000 2 = 30,000–100,000 3 = 10,000–29,000 4 = ≤10,000	4	2	2	1	1	1	2	3	3	3	4	4	1	4	3	1	4	1	1	2	1	1
		Pop. Status	2	2	2	2	1	2	2	2	2	2	2	2	2	1	2	2	1	2	2	2	2	2
		Range Size (km ²)	3	2	3	1	1	2	2	3	3	3	3	3	3	1	3	1	1	3	1	1	1	1
Restricted Ranges	No. of Islands	1 = >30 or large landmass 2 = 11–30 3 = <10	3	2	1	1	1	1	1	3	2	2	3	3	1	3	3	1	3	1	1	1	1	1
		Localized or Dispersed	2	2	0	0	0	2	0	dd	0	1	0	1	0	1	0	1	0	0	0	0	0	0
Incubation Strategy	Coastal or Inland Arcs	0 = strictly Inland 1 = some coastal 2 = mostly coastal	2	2	1	1	0	1	1	1	dd	1	1	2	1	1	0	1	0	0	0	0	0	0
		Heat Source	2	2	0	0	0	1	0	dd	1	1	1	0	1	0	0	2	0	0	0	1	0	0
		Method Plasticity	3	2	3	2	3	1	3	dd	2	1	3	2	3	3	3	2	3	3	3	2	3	3
		Total Points Accrued			24	18	13	10	9	13	12	12	15	17	20	20	9	17	16	10	17	9	9	11

Table B 2. Trait groups, relevant traits, and scoring for level of exposure of megapodes to the manifestations of climate change. All measures of precipitation change and temperature increases are based on climate data provided by the Intergovernmental Panel for Climate Change (IPCC 2014). Species for which data are deficient is indicated with “dd”.

EXPOSURE				Scrubfowl Clade													Brush-Turkey Clade									
Trait Group	Trait	Scoring	Tot. pos.	MO ME	SU ME	PH ME	NG ME	ME ME	DU ME	BI ME	MI ME	VA ME	NI ME	PO ME	OF ME	TA ME	MA LE	WA BT	WG BT	AU BT	MA LL	RB BT	BB BT	CO BT		
Sea Level Rise	Threat to breeding habitat	0 = not exposed 1 = min. exposed 2 = mod. exposed 3 = highly exposed	3	3	2	1	0	1	2	dd	2	2	2	3	1	1	0	2	0	0	1	1	1	2	1	
	Total Annual Increase	0 = no increase 1 = ≤ 100 mm 2 = 101–300 mm 3 = ≥ 300 mm	3	0	0	2	3	2	1	2	2	1	2	1	1	0	1	3	2	0	0	2	1	2		
	Total Annual Decrease	0 = no decrease 1 = ≤ 25 mm 2 = 26–50 mm 3 = ≥ 50 mm	3	2	2	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	2	1	0	0		
	Wet Season Increase	0 = no increase 1 = ≤ 100 mm 2 = 101–200 mm 3 = >200 mm	3	0	1	1	2	2	1	2	2	2	2	3	1	1	1	1	2	2	1	0	1	1	2	
Change in Precip.	Wet Season Decrease	0 = no decrease 1 = ≤ 20 mm 2 = ≥ 20 mm	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0		
	Dry Season Increase	0 = no increase 1 = ≤ 20 mm 2 = > 20 mm	2	0	0	0	2	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	1		
	Dry Season Decrease	0 = no decrease 1 = ≤ 25 mm 2 = 26–50 mm 3 = ≥ 50 mm	3	1	2	0	0	3	1	2	0	2	2	2	2	1	0	1	0	3	1	1	0	1	0	
	Yearly Mean Increase	0 = no change 1 = ≤ 1.0 C 2 = 1.1–2.0 C 3 = ≥ 2.1 C	3	3	3	3	3	3	3	3	3	3	3	3	2	3	3	3	3	3	3	3	3	3	3	
Change in Temp.																										
Total Points Accrued			22	10	10	7	10	11	8	9	9	10	13	7	7	8	8	10	10	8	7	8	8	9		

Table B 3. Trait groups, relevant traits, and scoring for level of adaptive capacity of megapodes to the manifestations of climate change. These data were gleaned through review of published literature presented in Table B14. Species for which data are deficient is indicated with “dd”.

ADAPTIVE CAPACITY				Scrubfowl Clade												Brush-Turkey Clade								
Trait Group	Trait	Scoring	Tot. pos.	MO ME	SU ME	PH ME	NG ME	ME ME	DU ME	BI ME	MI ME	VA ME	NI ME	PO ME	OF ME	TA ME	MA LE	WA BT	WG BT	AU BT	MA LL	RB BT	BB BT	CO BT
Adult Dispersal Ability	Extrinsic Barriers to Dispersal	0 = not isolated 1 = moderately isolated 2 = greatly isolated	2	1	1	0	0	1	1	1	2	2	1	2	0	1	1	0	1	0	2	0	0	0
	Total Points Accrued			1	1	0	0	1	1	1	2	2	1	2	0	1	1	0	1	0	2	0	0	0

Table B 4. Climate change vulnerability scores for the megapodes. Scores are calculated for each species by multiplying the sum of Sensitivity and Adaptive Capacity by Exposure.

		Scrubfowl Clade														Brush-Turkey Clade							
Assessment Category	Tot. Possible by Category	MO ME	SU ME	PH ME	NG ME	ME ME	DU ME	BI ME	MI ME	VA ME	NI ME	PO ME	OF ME	TA ME	MA LE	WA BT	WG BT	AU BT	MA LL	RB BT	BB BT	CO BT	
		18	13	10	9	13	12	12	15	17	20	20	9	17	16	10	17	9	9	11	9	10	
		1	1	0	0	1	1	1	2	2	1	2	0	1	1	0	1	0	1	0	0	0	
		10	10	7	10	11	8	9	9	10	13	7	7	8	8	10	10	8	7	8	8	9	
		29	24	17	19	25	21	22	26	29	34	29	16	26	25	20	28	17	17	19	17	19	
Total																							
Vulnerability Score		190	140	70	90	154	104	117	153	190	273	154	63	144	136	100	180	72	70	88	72	90	

Table B 5. Trait groups, relevant traits, and scoring for the level of other extrinsic threats to megapodes across their ranges.

EXTRINSIC THREATS				Scrubfowl Clade														Brush-Turkey Clade							
Trait Group	Trait	Scoring	Tot. pos.	MO ME	SU ME	PH ME	NG ME	ME ME	DU ME	BI ME	MI ME	VA ME	NI ME	PO ME	OF ME	TA ME	MA LE	WA BT	WG BT	AU BT	MA LT	RB BT	BB BT	CO BT	
Additive or Other Extrinsic Threats	Introduced Predators	0 = no reported threats 1 = minimal threats 2 = multiple threats	2	1	2	0	0	0	0	1	2	2	1	2	0	0	1	0	2	1	2	0	0	0	
	Anthropogenic	0 = no reported threats 1 = ≤2 threats 2 = 3–4 threats 3 = ≥5 threats	3	3	3	1	0	2	0	2	2	3	3	1	0	1	3	1	2	1	3	2	0	0	
	Stochastic	0 = no reported threats 1 = 1 threat 2 = 2–3 threats	2	1	0	0	0	0	0	0	2	2	2	1	2	0	0	1	1	1	0	1	0	0	
	Total Points Accrued			5	5	1	0	2	0	3	6	7	5	5	0	1	5	2	5	2	6	2	0	0	

Table B 6. Trait groups, relevant traits, and scoring for level of anthropogenic conservation actions underway or proposed to protect megapodes across their ranges.

CONSERVATION ACTIONS				Scrubfowl Clade												Brush-Turkey Clade								
Trait Group	Trait	Scoring	Tot. pos.	MO ME	SU ME	PH ME	NG ME	ME ME	DU ME	BI ME	MI ME	VA ME	NI ME	PO ME	OF ME	TA ME	MA LE	WA BT	WG BT	AU BT	MA LL	RB BT	BB BT	CO BT
Conservation Actions	Current of Underway	0 = no cons actions 1 = 1-2 cons actions 2 = 3-4 cons actions 3 = 5-6 cons actions	3	2	0	0	0	1	0	1	3	2	2	2	0	1	3	1	1	1	3	1	1	1
		Proposed	3	2	2	1	0	1	0	2	2	2	3	3	0	1	2	0	2	0	2	0	0	0
	Total Points Accrued		6	4	2	1	0	2	0	3	5	4	5	5	0	2	5	1	3	1	5	1	1	1

Table B 7. Data pertaining to populations, geographic and movement patterns, and diet for 21 species of megapodes assessed in Chapter 2. Under IUCN status, E = Endangered, V = Vulnerable, NT = Near Threatened, and LC = Least Concern.

Species	IUCN Stat.	Pop. Trend	Global Pop. Est.	Current Range	Range Size (km ²)	Elevation Range (m)	Movement Patterns	Diet
MOME	V	↓	20K-50K	E/C Indo; end. to Moluccas	49,331	0-2,000 (typ. >750)	Non-Mig	-
SUME	V	↓	15K-30K	C Indo; end. to Banggai and Sula Is.	4,293	450	Non-Mig	dd
PHME	LC	↓	-	PL, and E Borneo	457,463	≤ 2,000	-	Worms, grubs, termites, seeds, and fruit
NGME	LC	S	-	New Guinea	239,676	≤ 2,950	-	dd
MEME	LC	↓	-	Bism. Arch. and Solomons	84,875	≤ 1,500	-	plant materials, seeds, fruits, snails, worms, insects, crawfish
DUME	LC	↓	-	E/C Indo., PNG, Moluccas	59,731	≤ 450	-	Inverts (from one specimen only)
BIME	V	↓	3.5K-15K	Indo; end. Geelvink Bay Is.	2,948	≤ 450	Non-Mig	dd
MIME	E	↓	2K-2.5K	Mariana and Palau Is.	838	0-450	Non-Mig	seeds, insects, crabs, and plant matter
VAME	V	↓	3.5K-15K	End. to Vanuatu	6,452	0-800	Non-Mig	Worms, snails, seeds, fruits
NIME	V	↓	750-1.5K	End. to Nicobar Is., India	1,578	0-600	Non-Mig	Land snails, seeds, vegetable matter, insects, other inverts
POME	E	↓	680-970	End. to Tonga	70	-	Non-Mig	Insects and worms, small reptiles, seeds, small fruits
OFME	LC	S	100K-1M	N. Aus, NG, Indo., Timor Leste	795,557	0-1,800	Non-Mig	Insects, snails, larvae, fruits, young snakes, scorpions, seeds
TAME	NT	↓	1K-10K	End. to Tanimbar Is., Indo.	3,226	-	Non-Mig	dd
MALE	EN	↓	12K-21K	End. Sulawesi	146,297	0-1,056	Non-Mig	Fruits, seeds, inverts including insects, snails, scorpions
WABT	LC	S	6.7K-670K	PNG, West Papua	193,721	300-2,700	-	Fruit, seeds, probably insects
WGBT	EN	↓	977-1.4K	C. Indo., end. to Waigeo Is.	839	> 600	Non-Mig	One bird observed eating seeds
AUBT	LC	↓	-	N/E Aus.	642,774	-	-	Seeds, fruits, berries, vegetable matter, inverts, some small vertebrates
MALL	V	↓	100K-150K	C/S Aus	628,984	-	Non-Mig	Herbs, seeds, flowers, fungi, tubers, inverts, agr. stubble
RBBT	LC	↓	670-67K	West Papua, Moluccas	122,106	≤ 1,600	-	dd
BBBT	LC	↓	6.7K-670K	PNG, West Papua, Aru Is.	284,372	Usually < 100, but ≤ 800	-	Insects, small lizards, seeds, grubs, fallen fruit
COBT	LC	↓	6.7K-670K	PNG, West Papua	209,937	≤ 1,800	-	dd

Table B 8. Compilation of breeding data for 21 species of megapodes assessed in Chapter 2. Under incubation methods, MD = Microbial Decomposition, G = Geothermal, and PS = Passive Solar Radiation.

Species	Breeding Season	Nesting Areas		Incub Method			Clutch Size or Similar	Notes on Nesting	Gen. Length (yrs)
		Coast	Inland	MD	G	PS			
MOME	Year rnd, peak dry seas (Oct-Apr/May)	X	-	-	?	X	-	Lays nocturnally on sun-exposed beaches. Avoids laying during darkest period of moon.	4
SUME	dd, but likely Oct through Dec	X	X	X	-	-	-	-	4
PHME	Likely year rnd	X	X	X	-	-	.-	Will use beaches, prefers rotting treefalls in forest	-
NGME	Likely year rnd, may peak Jan to May	-	-	X	-	-	-	-	-
MEME	Apr-Nov, possibly to Jan	X	-	X	X	X	12 - 13 eggs every 9-20 d	-	-
DUME	May-Jul/Sept, Nov-Jan	X	X	X	-	-	-	-	-
BIME	dd	dd	dd	dd – presumed MD			-	-	-
MIME	Likely year rnd	X	X	X	X	-	-	-	4
VAME	Likely year rnd	X	X	X	X	X	-	No mounds found on volcanic island of Ambrym, but other strategies found	4
NIME	Dry seas, Nov or Dec-Apr	X	-	X	-	-	-	≥ 65% of mounds used by more than one breeding pair, a mean of 2.3±3.0 pairs / mound	4
POME	Likely year rnd, no clear peak	X	X	?	X	-	11.6-16.4 eggs / yr, 14-16 d interval	-	4
OFME	Year rnd across range	X	X	X	-	-	-	Builds the largest mound, nests communally, mounds recorded in continual use for over 40 yrs	4
TAME	dd	-	X	X	-	-	-	-	4
MALE	Year rnd, peak Oct-May	X	X	-	X	X	-	Burrows in volcanic soils, sun exposed beaches, lake shores, river banks, dirt roads along coastal areas	16
WABT	-	-	X	X	-	-	-	-	-
WGBT	-	-	X	X	-	-	-	-	13.5
AUBT	May/June-Jan/Feb	-	X	X	-	-	up to 24 eggs a season	-	-
MALL	Jun-Feb	-	X	X	-	-	Up to 30+ eggs / seas., 8-10 chicks / yr.	Relies on MD when moist organic matter is available, converts to PS when dry	16.8
RBBT	-	-	X	X	-	-	-	-	-
BBBT	Mostly Oct-May	-	X	X	-	-	-	Mound often at base of large tree on well drained, level ground in forest. May be used for several years before abandoned	-
COBT	Likely year rnd	-	X	X	-	-	up to 17 eggs / seas.	-	-

Table B 9. Habitats / cover types used by the 21 species of megapodes assessed in Chapter 2. I = important, S = suitable, and M = marginal.

Species	FOREST										SCRUBLAND				SHRUBLAND				Notes
	MM	ML	SW	D	T	SM	De	DS	IW	SCRUBLAND		SHRUBLAND							
										M	D	D	M	T	CS	PA	RG		
MOME	I	S	-	-	-	-	M	-	-	-	-	-	-	M	-	-	Also inhabits coastal scrub		
SUME	-	S	-	S	-	S	S	S	-	-	-	-	S	-	-	M	Prefers lowland coastal forest, regularly in dense scrub on the fringe of ag land and heavily degraded forest		
PHME	I	M	-	-	-	M	-	-	-	-	-	M	-	-	-	-	Uses secondary forest to some degree, may tolerate mildly disturbed habitat for foraging		
NGME	I	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
MEME	S	I	M	-	-	-	-	-	-	-	-	-	-	-	-	-	May use garden regrowth and hill forest		
DUME	-	S	I	-	-	I	-	-	S	-	-	-	-	-	-	-	-		
BIME	-	I	-	-	-	-	S	-	-	I	S	S	-	-	-	-	Regularly seen in disturbed habitat, otherwise relatively little info on habitat preferences		
MIME	I	I	-	-	-	-	-	-	-	S	-	-	-	-	S	S	Plantation in the form of old coconut forest		
VAME	-	I	-	-	-	-	M	-	-	-	-	-	-	-	-	-	Primarily lowland hill forest, believed to be poorly tolerant of degraded forest		
NIME	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Coastal forests important as primary nesting area		
POME	-	I	-	-	-	-	-	-	M	-	-	-	-	-	-	-	Inland wetlands generally geothermal in nature		
OFME	S	S	S	S	-	S	S	-	-	-	-	S	S	-	-	-	Dry forests and shrubland in coastal areas. Typically, more frequent at lower elevations, and tends to adapt well to secondary scrub		
TAME	-	I	-	-	-	-	S	-	-	-	-	-	-	-	-	-	Sparsely distributed throughout lowlands. Occurs in primary, old selectively logged and tall secondary, semi-evergreen forest		
MALE	S	S	-	-	-	M	-	-	S	-	-	-	-	-	S	-	-		
WABT	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
WGBT	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
AUBT	M	S	-	I	-	-	-	S	-	-	S	-	S	-	-	-	M		
MALL	-	-	-	S	S	-	-	S	-	-	S	-	-	S	-	-	Semi-arid to arid shrub and woodland dominated by mallee eucalypts and / or wattles		
RBBT	-	I	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-		
BBBT	-	I	-	-	-	-	M	-	-	-	-	-	-	-	-	-	-		
COBT	I	I	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-		

Table B 10. Known extrinsic (deterministic and stochastic) threats to the 21 species of megapodes assessed in Chapter 2.

DETERMINISTIC															STOCHASTIC			
Species	Def	HF	FDD	ASF	EC	Hun	IP	IC	Oth	Notes	V	F	T/C	Oth	Notes			
MOME	X	X	-	X	X	X	X	-	X	Overharvest of eggs main reason, sand mining threatens nesting grounds	-	-	-	X	Natural predation by local predators			
SUME	X	X	-	X	X	X	X	X	-	Feral and domestic fowl serve as comp., largely threatened by commercial logging	-	-	-	-	-			
PHME	X	-	-	X	-	-	-	-	-	Threatened in Sulawesi by logging	-	-	-	-	-			
NGME		-	-	-	-	-	-	-	-	-	-	-	-	-	-			
MEME	X	-	-	-	X	-	-	-	X	Clear cutting major threat, also egg over-harvesting	-	-	-	-	-			
DUME	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
BIME	X	-	-	X	X (?)	X	X	-	-	Much of forest on islands logged, converted to ag, or under pressure	-	-	-	-	-			
MIME	-	-	X	-	X	X	X	X	X	Marianas: ungulates and BTS. Palau: nest disturbance by tourists	X	-	X	-	Forest deg. via typhoons, volcanic activity in N. Mariana Islands			
VAME	X	-	X	X	X	X	X	X	?	Commercial sale of eggs and habitat loss	-	X	X	X	Storm waves and tsunami threats			
NIME	X	-	-	X	X	X	X	-	X	Ag, urbanization, mining, disease from domestic fowl, over hunting	-	-	-	X	Storm waves and tsunami threats			
POME	-	-	-	-	X	X	X	X	-	Over-harvesting of eggs primary reason for decline	X	-	-	X	Natural shift in geothermal activity			
OFME	-	-	-	-	-	-	X	-	-	Feral pigs threat to eggs across parts of range	-	-	-	X	Natural predation by local predators			
TAME	X	-	-	-	-	X	-	-	-	Declining due to habitat loss, exploitation	-	-	-	-	-			
MALE	X	X	X	X	X	X	X	-	-	Numerous; hab. loss, egg collecting, ag, urbanization, etc.	-	-	-	-	-			
WABT	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-			
WGBT	-	-	X	-	-	X	X	X	X	Cobalt, nickel mining, reduction in size of an existing reserve.	-	-	-	X	Climate change induced severe weather			
AUBT	X	-	-	-	-	-	X	-	-	-	-	-	-	-	-			
MALL	-	X	-	X	-	-	X	X	X	Incr. soil salinity, ag chemicals, road kills	-	X	-	-	-			
RBBT	-	-	X	-	X?	X?	-	-	-	-	-	-	-	-	-			
BBBT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
COBT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			

Table B 11. Current conservation actions established to protect 21 species of megapodes assessed in Chapter 2.

Species	LP	HM	SR	TR	HP	SC	CP	EP	Notes
MOME	X	X	X	X	-	-	-	-	Legal protection since 1979. Egg harvesting strictly controlled by traditional law - possible breakdown in traditional management, however, serves as serious threat to survival of these pops
SUME	-	-	-	-	-	-	-	-	No known conservation actions implemented
PHME	-	-	-	-	-	-	-	-	-
NGME	-	-	-	-	-	-	-	-	Nesting sites in West New Britain, Pokilli and Garu declared Wildlife Management Areas by PNG government. Restrictions on egg harvest was put in place in W. New Britain, but it was not clear if they were being adhered to
MEME	-	X	-	-	X	-	-	-	-
DUME	-	-	-	-	-	-	-	-	-
BIME	-	-	-	-	X	-	-	-	Protected areas on the islands, Biak-Utara and Pulau Supiori Nature Reserves, cover substantial areas of lowland and hill forest
MIME	X	-	X	X	X	X	X	-	Marianas: legally protected by USFWS in 1970, recovery plan drafted. Ungulates removed from Sarigan. Four N. Mariana Islands designated wildlife sanctuaries. Palau: Ngerukewid Islands Wildlife Reserve protects 50-80 birds, Rock Islands designated UNESCO WH site
VAME	X	X	X	-	-	-	-	X	Annual taboos on egg collecting, and monitoring protocols tested and baseline data collected on some islands. Due to cultural significance, great local interest in maintaining healthy pops.
NIME	X	-	X	-	X	-	X	-	Legally protected by Indian government in 1972 (ethnic tribes exempt from the Act). Prioritised by the Indian gov for preparation of a 'Species Recovery Plan'. Designation of most of Nicobars as tribal areas legally prohibits commercial exploitation of natural resources and settlement or ownership of land by non-tribals
POME	X	-	X	-	-	-	X	-	Legally protected by Tongan Government, but no enforcement. Past conservation effort (1991-1993) included egg translocation - later surveys showed that breeding was successful on both islands but longer term fate of chicks is unknown
OFME	-	-	-	-	-	-	-	-	-
TAME	-	-	-	-	X	-	-	-	-
MALE	-	-	-	-	-	-	-	-	-
WABT	-	-	-	-	X	-	-	-	Conservation sites identified over part of range
WGBT	-	-	-	-	X	-	X	-	Conservation sites identified over part of range, large reserve established in late 1980s
AUBT	X	-	-	-	X	-	-	-	Conservation sites identified over part of range
MALL	X	-	X	-	X	X	X	-	Captive breeding under way
RBBT	-	-	-	-	X	-	-	-	Conservation sites identified over part of range
BBBT	-	-	-	-	X	-	-	-	Conservation sites identified over part of range
COBT	-	-	-	-	X	-	-	-	Conservation sites identified over part of range

Table B 12. Conservation actions proposed to protect 21 species of megapodes assessed in Chapter 2.

Species	LP	HM	SR	IT	TR	HP	HR	SC	CP	EP	Notes
MOME	-	X	X	-	-	X	-	-	-	X	Determine effect of civil unrest on population status; determine the dispersal, range and movement of adults and chicks via radio-tracking and genetic studies
SUME	-	X	X	-	-	X	-	-	-	X	-
PHME	-	X	X	-	-	X	-	-	-	X	-
NGME	-	X	X	-	-	X	-	-	-	X	-
MEME	-	X	X	-	-	X	-	-	-	X	Recommended: intensive studies into breeding biology and dispersal and that careful consideration be given to habitat conservation and management
DUME	-	-	-	-	-	-	-	-	-	-	-
BIME	-	-	X	X	-	X	-	X	X	-	Assess habitat requirements and threats, status of forest on Biak-Supiroi, investigate breeding biology. Assessment of global status of the species
MIME	-	-	X	-	X	X	X	X	-	X	Throughout Range: detailed censuses, develop long-term monitoring programme, continue ecological research. Palau: determine risk of human disturbance to nest sites. Marianas: preserve remnant forest from development and feral ungulates
VAME	-	X	X	X	-	-	-	-	X	X	Investigation of productivity, dispersal and survival at nesting grounds. Implement egg harvesting restrictions during peak of breeding. Get locals to agree to implement taboo periods during which no eggs are to be collected.
NIME	X	X	X	-	-	X	X	X	X	X	Many proposed actions, including: further investigate breeding biology and habitat use, the impacts of changes in land-use patterns and the lifestyles of indigenous peoples
POME	-	X	X	X	X	X	-	X	-	X	Suggested ban on hunting and egg collecting, recommended local education and egg translocation programs
OFME	-	-	-	-	-	-	-	-	-	-	-
TAME	-	-	-	-	-	-	-	-	-	-	-
MALE	-	-	X	X	-	X	-	X	X	-	-
WABT	-	-	-	-	-	-	-	-	-	-	-
WGBT	X	-	-	-	X	-	-	-	X	X	-
AUBT	-	-	-	-	-	-	-	-	-	-	-
MALL	-	X	X	-	X	X	X	-	-	-	Various research projects are planned pertaining to demography, distribution, genetics, effect of agrochemicals.
RBBT	-	-	-	-	-	-	-	-	-	-	-
BBBT	-	-	-	-	-	-	-	-	-	-	-
COBT	-	-	-	-	-	-	-	-	-	-	-

Table B 13. Miscellaneous data and information used to assess the threats to 21 species of megapodes assessed in Chapter 2.

Species	Conservation Actions / Projects Proposed by Dekker et al. 2000	Data / Information Needs	General Notes
MOME	1.) Improve protection of nesting grounds; 2.) Initiate an effective conservation awareness program; 3.) Develop a system of sustainable harvest of eggs	Non-breeding season habitat and range	Baker 1999: Considered the most endangered species of megapode
SUME	-	Chicks little studied. Apparently little data on breeding seasonality.	-
PHME	-	-	Inansyah et al 2009 suggests that this species is Threatened (perhaps in Indonesia only). Sinclair et al. 2002 suggests it be listed as Vulnerable in Sulawesi
NGME	-	-	-
MEME	-	-	Broome et al. 1984: because birds disperse widely, they are susceptible to increased habitat destruction throughout New Britain
DUME	-	-	-
BIME	1.) Survey for species on Biak and surrounding islands to describe habitat requirements, measure population densities, and generate a global population estimate; 2.) formulate a conservation management plan for the species	Habitat preferences, general habits, diet or breeding biology; these, however, are thought to be broadly similar to other Megapodius species	-
MIME	Supports all conservation action proposed by the USFWS (1998) species recovery plan	Habitat preferences, general habits, diet or breeding biology; these, however, are thought to be broadly similar to other Megapodius species	-
VAME	1.) Initiate a sustainable egg harvesting program; 2.) Survey for the species on islands other than Ambrym and assess its tolerance of degraded forests and elevational distribution	Habitat preferences, general habits, diet or breeding biology; these, however, are thought to be broadly similar to other Megapodius species	Foster 1999: During the rainy season (November-April) cloud cover and rainfall reduced the temperature of the substrate and saturation of air spaces prevents gas exchange through the egg shell. Concluded that the number of laying females had not decreased between 1995 and 1996, but that the survival of eggs to sexually mature adults may have dropped due to the high levels of egg collecting.
NIME	1.) Improve protection of nesting habitat; 2.) Initiate an effective conservation awareness program; 3.) Continue monitoring of breeding population; 4.) Investigate demography / vital rates of species and do a minimum PVA	Habitat preferences, general habits, diet or breeding biology; these, however, are thought to be broadly similar to other Megapodius species	Sivakumar 2009: proposes, that since the population had decreased by ~70% since 1995 (due to the 2004 tsunami), and that habitat destruction and hunting are still adversely affecting the species, it probably qualifies to be listed as Endangered by IUCN

Table B 13. Continued

Species	Conservation Actions / Projects Proposed by Dekker et al. 2000	Data / Information Needs	General Notes
POME	1.) Monitor breeding populations on Niuafu'ou Island; 2.) Raise public awareness of the conservation of the species; 3.) Continue translocation of species to Late and Fonualei	-	-
OFME	-	Komodo National Park: data on the number of incubation mounds and habitat characteristics that influence their distribution is needed to facilitate informed decisions regarding scrubfowl management and conservation in KNP.	Inansyah et al 2009: up to 70% of female Komodo Dragons oviposit in Orange-footed Scrubfowl incubation mounds; thus, knowledge of nesting ecology of the megapode is important to the conservation and management of the dragon.
TAME	-	Estimates of species population size - last survey completed in 1991. Understudied. No data on voice or breeding seasonality. Little known or diet. Chicks little studied.	-
MALE	1.) Improved protection of nesting grounds on Sulawesi; 2) Conservation awareness program; 3.) Develop a system of sustainable harvesting of eggs	-	-
WABT	-	Research into population size, status, trends, distribution, life history and ecology, and threats	-
WGBT	1.) Survey for the species on Waigeo island; 2.) Draft management plan for its conservation	-	-
AUBT	-	-	-
MALL	Supports all conservation recommendations made by the National Malleefowl Recovery Team	-	-
RBBT	-	-	-
BBBT	-	-	-
COBT	-	-	-

Table B 14. Bibliography of published literature reviewed to determine the level of sensitivity, adaptive capacity, extrinsic threats to, and conservation actions for the Megapodiidae. Data gleaned from these publications were used to fill out Tables B7–B13, and to formulate my Trait-based Vulnerability assessment for the family as presented in Tables B1–B6, above, and in Chapter 2.

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Table B 15. Change values used to determine and assess the level of exposure of 21 species of megapode, detailed in Chapter 1. All values RCP 4.5 and 8.5 values are the mean of values for three climate change models; the Commonwealth Science and Industrial Research Organization's (CSIRO) ACCESS 1.0, University of Tokyo's National Institute for Environmental Studies MIROC 5, and Met Office Hadley Centre's HadGEM2-AO. 'Base' refers to the baseline values for each category taken from projections of 1980 to 2000 climate averages.

Mean Values for Access 1.0, Miroc 5, and HadGEM2 Models															
Species	Yearly Mean Temp			Max Temp / Warmest Month			Total Annual Precipitation			Wet Season Precipitation			Dry Season Precipitation		
	Base	Change by 2070		Base	Change by 2070		Base	Change by 2070		Base	Change by 2070		Base ^e	Change by 2070	
		RCP 4.5	RCP 8.5		RCP 4.5	RCP 8.5		RCP 4.5	RCP 8.5		RCP 4.5	RCP 8.5			
<i>M_tenimberensis</i>	27.1	1.7	2.3	32.4	1.7	2.4	1936	66	-157	784	50	44	70	17	7
<i>M_reinwardi / A_lahani</i>	26.0	1.9	2.6	33.2	1.6	2.4	1704	-50	-133	1160	-10	-10	21	2	2
<i>M_reinwardi / A_lahani</i>	23.0	1.8	2.6	30.9	1.8	2.5	2487	88	-78	1397	81	177	157	-28	-26
<i>M_reinwardi</i>	26.9	2.1	3.0	34.2	1.9	2.8	1197	65	-98	804	76	-36	2	0	0
<i>M_reinwardi</i>	27.2	2.2	3.1	36.2	2.1	3.1	1322	65	-75	846	70	-15	9	1	1
<i>M_reinwardi</i>	26.5	2.4	3.3	34.3	2.0	2.8	1288	50	-14	928	26	-20	17	0	-1
<i>M_reinwardi</i>	22.7	1.9	2.5	29.7	1.8	2.5	2245	-81	-148	1048	15	45	112	-18	-25
<i>M_reinwardi</i>	22.0	1.8	2.5	28.2	1.8	2.5	1513	-23	-89	770	22	15	76	0	-6
<i>M_reinwardi</i>	22.6	1.9	2.6	28.2	1.9	2.8	2248	-37	-128	1197	-7	25	114	-18	-25
<i>M_reinwardi / T_fuscrosiris</i>	26.5	1.7	2.4	31.3	1.7	2.4	2209	251	11	808	63	32	276	78	10
<i>M_reinwardi / T_fuscrosiris</i>	26.6	2.0	2.8	32.2	2.0	2.8	2975	366	57	962	103	61	494	60	-54
<i>M_reinwardi / T_fuscrosiris</i>	26.2	1.9	2.6	30.5	1.9	2.7	2802	205	194	860	95	92	543	6	14
<i>M_reinwardi / T_cuvieri</i>	26.7	1.8	2.4	31.3	1.8	2.3	2307	256	220	804	174	243	268	53	-30
<i>M_nicobariensis</i>	26.1	1.7	2.3	29.6	1.7	2.4	2026	66	79	900	36	30	269	12	4
<i>M_laperouse</i>	26.3	1.8	2.4	30.4	1.7	2.4	1701	23	-47	721	62	35	224	-6	-23
<i>M_laperouse</i>	26.4	1.7	2.3	30.6	1.7	2.4	2643	132	182	728	49	115	573	-10	-28
<i>M_geelvinkianus</i>	26.2	1.8	2.6	30.7	1.7	2.6	2197	277	194	782	150	130	376	28	11
<i>M_freycinet / E_wallacei</i>	23.5	1.7	2.5	28.4	1.7	2.5	1976	31	-154	789	-13	-122	287	12	-14
<i>M_freycinet / E_wallacei</i>	24.7	1.8	2.5	28.9	1.9	2.6	2721	154	-132	952	57	-67	420	21	-21
<i>M_freycinet / E_wallacei</i>	25.4	1.7	2.4	30.1	1.7	2.4	4108	108	253	1249	29	174	762	74	46
<i>M_erenia</i>	21.4	1.6	2.4	25.6	1.6	2.3	2834	174	237	851	66	161	598	40	0
<i>M_erenia</i>	25.1	1.6	2.2	29.9	1.6	2.2	3693	-39	160	966	147	320	876	-141	-236

Table B 15. Continued

Mean Values for Access 1.0, Miroc 5, and HadGEM2 Models															
Species	Yearly Mean Temp			Max Temp / Warmest Month			Total Annual Precipitation			Wet Season Precipitation			Dry Season Precipitation		
	Change by 2070			Change by 2070			Change by 2070			Change by 2070			Change by 2070		
	Base	RCP 4.5	RCP 8.5	Base	RCP 4.5	RCP 8.5	Base	RCP 4.5	RCP 8.5	Base	RCP 4.5	RCP 8.5	Base	RCP 4.5	RCP 8.5
<i>M. decollatus</i> / <i>T. jobiensis</i>	20.2	1.9	2.7	25.7	1.9	2.7	2976	245	477	916	37	116	608	85	123
<i>M. bernsteini</i>	26.5	1.7	2.3	31.6	1.8	2.5	2301	83	-69	826	49	20	302	-2	-44
<i>M. bernsteini</i>	26.0	1.9	2.5	31.2	1.8	2.6	1916	66	-28	735	41	41	274	-5	-47
<i>M. cumingii</i> / <i>M. maleo</i>	20.3	2.0	2.8	25.8	2.0	3.1	2351	-18	-136	756	19	14	334	-6	-33
<i>M. cumingii</i> / <i>M. maleo</i>	19.3	2.0	2.8	24.8	2.2	3.2	1960	158	143	628	90	91	296	24	10
<i>M. cumingii</i> / <i>M. maleo</i>	24.7	1.8	2.6	29.9	1.8	2.6	1872	67	-100	568	35	1	317	10	-23
<i>M. cumingii</i>	26.8	2.0	2.8	31.0	2.1	3.0	2707	206	152	793	72	84	595	27	-21
<i>M. cumingii</i>	24.3	1.8	2.6	29.1	1.9	2.7	2505	406	215	944	267	143	474	-9	-47
<i>M. cumingii</i>	23.0	2.0	2.8	28.7	2.0	2.6	2950	213	91	861	172	123	560	36	-24
<i>M. cumingii</i>	25.4	1.7	2.4	30.6	1.8	2.6	1967	176	198	861	37	40	68	28	40
<i>M. cumingii</i>	24.4	1.8	2.5	29.3	1.9	2.8	3112	727	523	1161	389	331	489	73	9
<i>M. cumingii</i>	27.1	1.8	2.5	33.6	1.8	2.6	2012	101	-54	795	57	45	99	5	0
<i>M. cumingii</i>	24.1	1.8	2.5	30.5	1.8	2.7	3137	290	100	1210	105	110	305	-32	-41
<i>M. laprouse</i>	26.8	1.7	2.3	30.8	1.7	2.4	3603	402	631	1190	176	314	599	41	23
<i>M. pritchardii</i>	26.3	1.4	2.0	30.5	1.5	2.2	2416	40	76	832	42	83	344	-38	-34
<i>M. layardi</i>	23.8	1.6	2.2	29.5	1.7	2.4	2336	216	61	965	77	115	334	13	-43
<i>M. eremita</i>	26.7	1.7	2.3	30.9	1.7	2.3	3780	120	137	1268	14	-64	741	2	44
<i>M. eremita</i>	24.8	1.7	2.3	29.2	1.6	2.2	3731	137	-172	1149	15	-6	775	39	-99
<i>M. reinhardt</i> / <i>T. fuscirostris</i>	26.4	1.9	2.8	32.6	1.9	2.7	2542	124	-61	921	66	25	349	-15	-60
<i>M. decollatus</i> / <i>T. jobiensis</i>	26.6	1.9	2.6	31.4	1.9	2.7	3183	124	315	1173	30	108	362	-5	-4
<i>M. reinhardt</i>	26.3	1.6	2.3	31.3	1.7	2.4	2506	-21	-195	781	8	-23	433	12	-34
<i>L. ocellata</i>	21.1	2.1	2.8	36.2	2.6	3.0	271	-41	-67	151	-31	-48	17	0	-1
<i>L. ocellata</i>	16.8	1.9	2.7	32.7	2.2	2.8	338	-29	-58	137	-9	-22	50	0	-13
<i>L. ocellata</i>	19.4	2.1	3.0	35.2	2.1	3.1	177	15	17	61	10	10	29	1	2
<i>L. ocellata</i>	17.3	1.7	2.5	30.4	1.9	2.9	289	3	-2	112	2	0	36	1	5
<i>L. ocellata</i>	16.9	2.0	2.8	32.6	2.4	3.4	292	-10	-13	89	3	-1	58	-4	-6

Table B 15. Continued

Mean Values for Access 1.0, Miroc 5, and HadGEM2 Models															
Species	Yearly Mean Temp			Max Temp / Warmest Month			Total Annual Precipitation			Wet Season Precipitation			Dry Season Precipitation		
	Base	Change by 2070		Base	Change by 2070		Base	Change by 2070		Base	Change by 2070		Base	Change by 2070	
		RCP 4.5	RCP 8.5		RCP 4.5	RCP 8.5		RCP 4.5	RCP 8.5		RCP 4.5	RCP 8.5			
<i>L_ocellata</i>	17.2	2.3	3.3	32.4	2.0	3.2	564	24	1	169	22	28	118	-7	-18
<i>A_luthami</i>	25.9	2.3	3.2	37.3	2.2	3.1	853	52	18	609	47	65	10	0	-2
<i>A_luthami</i>	22.1	2.1	2.9	32.3	2.0	2.7	821	-5	-3	439	22	86	52	-9	-10
<i>A_luthami</i>	20.3	2.3	3.3	33.2	2.3	3.1	674	9	-37	285	21	27	92	-6	-15
<i>A_luthami</i>	19.8	2.0	2.9	30.8	2.0	2.9	914	20	-66	362	31	12	119	-7	-10
<i>A_luthami</i>	14.8	2.2	3.1	26.8	2.1	3.0	964	35	52	378	61	58	121	-7	2
<i>A_luthami</i>	15.3	2.2	3.0	26.8	1.9	2.6	1040	25	60	366	34	60	154	-4	6
<i>A_bruijii / M_freyinet</i>	26.4	1.7	2.3	30.4	1.7	2.5	2748	223	203	963	135	158	521	-27	-49
<i>A_arfakianus</i>	18.0	1.8	2.6	24.0	1.8	2.5	3345	379	483	987	188	208	681	32	55
<i>A_arfakianus</i>	21.0	2.0	2.8	26.5	1.9	2.7	5092	636	1073	1370	219	407	1147	72	173
<i>A_arfakianus</i>	20.3	2.1	2.9	26.7	1.9	2.6	2078	70	220	706	25	101	283	-9	-24
<i>A_arfakianus</i>	13.4	1.7	2.5	20.5	1.7	2.7	2928	45	-46	1173	75	53	346	-12	-45
<i>A_arfakianus / M_reinwardt / T_cuvieri</i>	21.5	1.8	2.4	26.0	1.9	2.7	3160	198	245	935	128	180	648	-38	-46
<i>T_fuscirostris / T_jobensis / M_reinwardt</i>	26.0	1.8	2.5	32.0	1.8	2.6	1311	-12	-94	515	18	3	164	-24	-38
<i>T_cuvieri / T_fuscirostris</i>	26.5	1.8	2.5	31.0	1.9	2.7	2723	293	200	838	82	51	450	103	69
<i>M_reinwardt / T_cuvieri / T_fuscirostris</i>	26.1	1.8	2.5	31.4	1.8	2.6	3429	347	253	1131	165	75	603	42	22
<i>T_jobensis / M_reinwardt / M_decollatus</i>	26.7	1.7	2.5	32.2	1.7	2.5	3304	206	207	1129	175	234	512	-16	-69
<i>M_maleo</i>	21.8	2.0	2.9	27.3	2.1	3.2	2950	148	80	1011	60	59	426	26	-1
<i>M_cumingii</i>	25.9	1.9	2.7	30.7	1.8	2.8	2317	250	115	757	140	64	462	35	-5
<i>M_cumingii</i>	26.4	1.8	2.5	32.7	1.8	2.5	1689	163	198	602	26	33	239	79	99
<i>M_cumingii</i>	26.5	1.9	2.7	32.0	2.0	2.7	2298	206	69	987	-4	-64	165	27	40
<i>M_cumingii</i>	24.0	1.8	2.5	28.9	1.9	2.8	1724	243	209	651	98	128	132	35	19
<i>M_reinwardt</i>	22.6	1.7	2.4	28.1	1.6	2.3	1307	-69	-163	591	15	0	36	5	9

